SHRINKING BOREAL LAKES AS AGENTS OF CHANGE: UNTANGLING STRUCTURE AND FUNCTION IN HYDROLOGICALLY-COUPLED LAKES AND WETLANDS

By

Vijay P. Patil, M.S.

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Approved:

Brad Griffith, Committee Chair
Eugénie Euskirchen, Committee Co-Chair
Mark Waldrop, Committee Member
A. David McGuire, Committee Member
Kris Hundertmark, Chair,
Department of Biology and Wildlife
Anupma Prakash, Interim Dean
College of *Natural Science and Mathematics*
Michael Castellini, *Dean of the Graduate School*

Abstract

Widespread lake shrinkage has occurred over the last 30 years throughout interior Alaska and other boreal regions. This trend has been broadly linked to climate change, via multiple proximate drivers including permafrost thaw, shifting water balance, and terrestrialization caused by peat growth. The ecological effects of shrinking boreal lakes are still poorly understood. I used space-for-time substitution based on field surveys from a spatially balanced random sample of lakes (n=130) to examine the implications of shrinking lakes in the lowland floodplain of the Yukon River within the Yukon Flats National Wildlife Refuge in northern Alaska. Historical lake shrinkage over the last 30 years increased plant functional diversity, woodiness and above-ground biomass in lake-margin wetlands, despite a significant loss of wetland and lake area. Shrinking lakes appeared to have decreased hydrological connectivity with surrounding wetlands, and reduced organic carbon and nitrogen inputs from the surrounding landscape. However, land cover and bathymetry were better predictors of water chemistry than lake shrinkage. Continued reductions in lake surface area, combined with terrestrial succession, may reduce wetland area and increase the relative abundance of woody wetland vegetation compared to herbaceous plants. Lake shrinkage could also reduce below-ground C stocks, because lake sediments contain more organic C per m^2 than terrestrial soils, and lake sediment C appears vulnerable to aerobic decomposition. Overall, lake shrinkage will most likely affect plant and animal biodiversity, waterfowl and wildlife habitat quality, and C storage in contrasting ways, and management of drying landscapes may require difficult tradeoffs to be made as a result. These decisions would be aided by process-based modeling that accounts for the role of plant functional traits and explicitly represents hydrological interaction between terrestrial and freshwater ecosystems.

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Chapter 1 : General Introduction

Lakes and the landscapes that surround them are linked through ecohydrology, which is an emerging field of research into interaction between hydrological and biological processes and their combined influence on ecosystem structure and function (Rodriguez-Iturbe 2000). Lake water balance, water chemistry, and productivity are influenced by terrestrial plant communities and soils, through multiple mechanisms that include evapotranspiration, soil infiltration, organic matter decomposition, and nutrient leaching through groundwater flow (Grimm et al. 2003, Cole et al. 2007, Roach et al. 2011). Lakes can also influence terrestrial ecosystem structure and function, including land cover, biodiversity, biomass production, and soil carbon (C) storage, through ecohydrological mechanisms that include soil moisture and thermal dynamics, flooding disturbance, nutrient cycling, and local climate regulation (Larmola et al. 2004, Jorgenson and Shur 2007, Minsley et al. 2012).

Ecohydrology can help us to understand the feedback mechanisms that influence ecosystem responses to climate change (Rodriguez-Iturbe 2000, Walvoord and Striegl 2007, Chapin et al. 2009, McGuire et al. 2009). For example, anthropogenic warming can affect multiple pathways for movement of water among soil, vegetation, and the atmosphere, including the timing and magnitude of precipitation as well as soil moisture loss through drainage/runoff, evaporation, and transpiration (Hay and McCabe 2010). These responses can alter C cycling by affecting organic matter decomposition, plant growth and biomass production, fire regimes, and methane production (which is associated with saturated/anoxic conditions in soils and lake sediments) (Zhuang et al. 2004; Chapin et al. 2009; Jorgenson et al. 2013; Prowse et al. 2006; D'odorico et al. 2010; Coletti et al. 2013). Widespread changes in precipitation and soil moisture can also influence the distribution and abundance of plants at multiple scales, from lakeshores to

landscapes to biomes (Rochefort et al. 1994, Chapin et al. 2009, Myers-Smith et al. 2011, Sulman 2012, Aubin et al. 2016). Shifts in plant community structure, diversity, and distribution can in turn alter the resilience of communities to future disturbance events such as burning and flooding, and send those communities onto new successional trajectories (Lavorel and Garnier 2002, Elmqvist et al. 2004).

Arctic and boreal landscapes have experienced dramatic hydrological changes over the last few decades, including a net reduction in lake size and total lake surface area (Yoshikawa and Hinzman 2003, Smith et al. 2005, Riordan et al. 2006, Roach et al. 2011). In boreal Alaska, these trends have been linked to a combination of factors including permafrost thaw leading to subsurface drainage, increased evapotranspiration, and the conversion of lakes to peatlands through terrestrialization (Yoshikawa and Hinzman 2003, Klein et al. 2005, Roach et al. 2011). All of these mechanisms are associated with a warming climate, and because high latitudes are continuing to warm more rapidly than the rest of the world, lake shrinkage could become an increasingly widespread phenomenon (Berner et al. 2005). Climate change is also projected to affect precipitation patterns at high latitudes, including the volume of winter snowpack and the phenology of spring snowmelt and ice breakup, and these changes could contribute to increase spatial and temporal variability in lake size (Ernakovich et al. 2014).

Widespread lake shrinkage could have ecological consequences at local, regional, and global scales. Because permafrost and seasonally frozen soils impede drainage, freshwater lakes are ubiquitous features of circumpolar landscapes (Jorgenson and Shur 2007, Edwards et al. 2016). Boreal lakes range in size from less than 1 hectare to millions of hectares (Schindler et al. 1996, Kortelainen et al. 2004, Rover et al. 2012). This diversity helps shape boreal lowlands into complex mosaics of freshwater, upland vegetation, and mixed woody and herbaceous wetlands

(USFWS 1987, Gallant et al. 1995, Jorgenson et al. 2013), which provide breeding habitat for millions of migratory waterfowl, shorebirds, and furbearers. Lakes and wetlands also store a substantial fraction of all boreal and arctic organic C, due to a combination of cold, saturated, and anoxic soils that slow decomposition and allow soil organic matter to accumulate (Kortelainen et al. 2004, Benoy et al. 2007). As lakes and wetlands shrink, their stored C could become increasingly vulnerable to decomposition and respiration as carbon dioxide (CO_2) or methane (CH_4), both of which are potent greenhouse gases (McGuire et al. 2009). Long-term reductions in lake and wetland size could therefore alter regional C fluxes between boreal soils and the atmosphere. Lake surface area change is therefore potentially important as both a driver of local and regional biodiversity and as a climate feedback mechanism.

Despite a substantial body of research assessing the mechanisms behind boreal lake surface area losses (Roach et al. 2011, Chen et al. 2012, Roach et al. 2013), little is known about their ecological effects. In this dissertation, I examined the effects of boreal lake shrinkage on community structure, biodiversity, productivity, water chemistry, and C cycling. My work was part of a larger effort to understand the implications of climate change for biodiversity within the Yukon River basin (YRB). I focused specifically on the Yukon Flats National Wildlife Refuge (YFNWR) in Northern Alaska, where rapidly shrinking lakes are common features of the landscape (Roach et al. 2013; Rover et al. 2012). The YFNWR encompasses 3.5 million hectares of boreal lowlands and loess hills straddling the northernmost portion of the Yukon River (USFWS 1987). Despite receiving less than 10 inches of precipitation annually, including rain and snow (Drury and Grissom 2008), the floodplain occupying the central YFNWR contains thousands of lakes and wetlands, which are maintained by the presence of poorly-drained permafrost soils (Gallant et al. 1995). This diverse landscape is subject to frequent disturbance in

the form of flooding and wildfire (Gallant et al. 1995). The soils, which are primarily alluvial deposits and aeolian loess, are characterized by a north-south gradient of continuous to discontinuous permafrost (Brabets et al. 2000, Jorgenson et al. 2008). This natural variability in disturbance regime, vegetation, and soil properties within a single climatic ecoregion (The Yukon Flats Ecoregion; Gallant et al. 1995) makes the YFNWR ideal for examining the ecological interplay of climate and hydrology.

There is a compelling need to understand the effects of lake shrinkage in the YFNWR, where the protection of natural diversity of plants, animals, and their habitats is mandated by federal law (Meretsky et al. 2006), and where the residents of seven local villages live a largely subsistence lifestyle dependent on having access to clean natural water sources, healthy ecosystems, and robust wildlife populations (USFWS 1987, Lanen et al. 2012). While C storage was not targeted for management in the original legislation that established National Wildlife Refuges, it is increasingly recognized as a climate regulation ecosystem service provided by federal lands (Ingraham and Foster 2008, Patton et al. 2015). Understanding how lake shrinkage affects the landscape of the YFNWR could help inform how this public resource and the services it provides are managed in the face of future climate change. In addition, YFNWR lakes represent the same diversity of lake surface area trends observed across the entire state of Alaska (Roach et al. 2013). This means that lake and wetland responses to lake shrinkage in the YFNWR provide a glimpse of what could be in store for all of the YRB, which encompasses over 85 million hectares and is home to over 100,000 people (Brabets et al. 2000), and for the 19.5 million hectares of Alaska protected in 11 National Wildlife Refuges (USFWS 2015).

I conducted three studies that examine how climate-mediated changes in lake surface area affect interactions between boreal lakes and the surrounding terrestrial plant communities. In

each study, I also attempted to place the effects of lake surface area change in a broader context by contrasting them with the effects of other landscape characteristics such as fire disturbance. In **Chapter 2**, my objective was to evaluate whether relationships among lake dynamics, wildfire, and wetland C stocks were influenced by plant functional diversity (the distribution of plant traits which affect ecological function). I also tested alternative hypotheses about the relative importance of three functional diversity components (functional composition, functional divergence, and idiosyncratic species; Díaz et al. 2007). I fit structural equation models using data from a survey of plant biodiversity at 130 lakes, field measurements of C stocks, and a database of plant functional traits (Kattge et al. 2011). In **Chapter 3**, I asked whether drying and flooding histories for individual lakes could be used to predict summer water chemistry. Specifically, I tested whether lake dynamics mediated the influence of other landscape characteristics (e.g., land cover, soil type, permafrost, disturbance history, and lake-specific physical characteristics) on water chemistry, using random forest regression tree models (Cutler et al. 2007). Finally, in **Chapter 4** I projected past and future lake size, wetland size, and wetland community composition and biodiversity using Monte Carlo simulations that accounted for spatial variability (Roach and Griffith 2015). I parameterized these simulations from field measurements at a spatially balanced random sample of lakes and wetlands (Stevens and Olsen 2004; Roach and Griffith 2015), which allowed me to estimate the effects of lake size dynamics on wetland size, wetland plant community characteristics (above-ground biomass and biodiversity), and lake and wetland C stocks across the central lowland floodplain of the YFNWR while accounting for the influence of other landscape characteristics such as fire/disturbance regimes. I also generated future projections to the year 2100. I based these projection on lake trends in three Yukon Flats sub-regions characterized by 1) a small significant

increasing trend in lake size, 2) rapid, significant, and large reduction in lake size, and 3) high year-to-year variability in lake size. My objective for this analysis was to assess the effects of lake shrinkage on the size of individual wetlands as well as total lake and wetland surface area. I also combined land cover projections with estimates of soil C stocks associated with boreal wetlands (measured) and lakes (derived from the literature) to infer the potential effects of lake shrinkage and wetland succession on regional C storage.

Boreal lowland regions such as the Yukon Flats are shaped by the twin forces of fire and water (Gallant et al.1995). While boreal wildfire has been extensively studied, the mechanisms causing long-term change in lake size and the consequences to local ecosystems are still poorly understood. In this dissertation, I examined the responses of wetland plant communities, soils, and lake ecosystems to historical lake shrinkage and flooding, while testing alternative hypotheses regarding how those responses were shaped by terrestrial/aquatic interactions. Collectively, these analyses help quantify the implications of continued warming and lake change for boreal landscapes and for the resources they provide.

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Chapter 2 : Biodiversity as a mediator of disturbance effects on carbon storage in boreal lake-margin plant communities[1]

Abstract

Long-term warming trends are expected to alter the frequency and intensity of disturbances in boreal Alaska, and predicting the ecological consequences of warming requires a clear understanding of how disturbance regimes influence ecosystem function. Lake shrinkage may represent an important new component of local disturbance regimes that has the potential to influence ecosystem function and carbon storage in adjacent wetlands, but the effects of disturbance on carbon storage may be mediated by the distribution of wetland plant functional traits. I fit structural equation models with field data from the Yukon Flats National Wildlife Refuge to test whether relationships among disturbance regimes (fire history and lake shrinkage trends) and carbon stocks (aboveground biomass and soil organic content) were influenced by plant functional diversity. The effects of lake shrinkage on wetland C storage were statistically independent of the effects of fire history, but were comparatively small. Above-ground plant biomass was highest in small wetland zones surrounding rapidly shrinking lakes, and was positively correlated with plant functional trait divergence (variability in trait distribution and abundance) while soil organic layer thickness was positively correlated with the abundance of functional traits linked to woody vegetation. These results suggest that wetland plant biomass at shrinking lakes was influenced by the encroachment of woody shrubs into herbaceous wetlands via succession. Results also implied that the distribution of a few species, representing unique trait assemblages, can significantly affect ecosystem function. Consideration of the ecological role played by plant functional diversity could improve our ability to model ecosystem responses

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to disturbance, and could help inform management decisions by clarifying the ecological and social value of plant community characteristics.

Introduction

At high latitudes, the effects of climate warming are expected to include increasingly frequent and intense disturbances (Soja et al. 2007). In boreal ecosystems, the primary disturbance agent is wildfire, which is a major determinant of plant community composition, successional dynamics and organic carbon (C) stocks (Balshi et al. 2007; Jonsson and Wardle, 2010; O'Donnell et al. 2011). Warming has also been linked to reductions in lake size and abundance throughout the circumpolar north over the last 50 years (Roach et al. 2011). Lake shrinkage has been frequently observed in Alaskan National Wildlife Refuge lands, which contain thousands of lakes and wetlands that have been set aside to preserve their "biological integrity, diversity and health" (Meretsky et al. 2006). Shrinkage trends vary across the state, but some boreal Alaskan refuges have lost an average of 3% of their surface water per year since 1980 (Roach et al. 2013). Lakes are more likely to have dried in areas that have burned in recent decades, but other variables including soil type and proximity to rivers were also important (Roach et al. 2013). Sustained lake shrinkage could be an important new influence on ecosystem dynamics in the surrounding landscape (Riordan et al. 2006).

Boreal lakes have strong hydrological ties with lake-margin wetlands, which are regions of saturated or seasonally water-covered land that are typically occupied by hydrophilic plant communities (Cowardin et al. 1979). Lake shrinkage could therefore be associated with losses in wetland area (Whitehouse and Bayley 2005). Lakes and lake-margin wetlands provide critical waterfowl breeding habitat, and reductions in their abundance are projected to drive local and regional declines in waterfowl diversity (Roach and Griffith 2015). Lakes and wetlands are also a major component of local and global C budgets (Molot and Dillon 1996; Benoy et al. 2007). A recent synthesis paper estimated that the boreal region contained a total C stock of 1095 Pg

(Bradshaw and Warkentin 2015), and as much as two thirds of that C may be contained in lake sediments and organic-rich peat soils composed of partially decomposed vegetation (Gorham et al. 1991; Benoy et al. 2007). By comparison, total terrestrial C stocks have been estimated at between 1330 and 1580 Pg for all permafrost-containing regions (Hugelius et al. 2014), and 2050 Pg for surface soils in the rest of the world combined. Peat layers are strongly affected by the accumulation, death, and decomposition of above-ground biomass (AGB; Chapin et al. 2009; Conti and Díaz, 2013), which also provides forage and/or cover for wildlife. The rate of AGB production is quadratically related to soil moisture, such that peat accumulation is promoted by a combination of low temperatures and saturated, anoxic wetland soils, which impede decomposition (Gorham 1991; Chapin et al. 2011). In other words, lake shrinkage and associated reductions in wetland soil moisture have the potential to affect C budgets above and below ground.

Shrinking lakes could also have more subtle effects on wetland communities. Boreal wetlands are local plant biodiversity hotspots, including species and growth forms that cannot be found in more abundant upland forest habitat (Whitehouse and Bayley 2005). Species diversity generally increases as a function of area (Whittaker and Triantis 2012), and site-specific plant species diversity could increase in response to lake shrinkage as lake-margin wetlands expand into newly exposed bare soil. However, local species losses could also occur as lake shrinkage changes soil physical properties (moisture, pH, etc.). Lake-shrinkage effects on wetland plant species richness and evenness are currently unknown, and it is difficult to predict whether such local effects might be sufficient to alter diversity at larger scales in boreal lowlands (Whittaker et al. 2001). The necessary data for assessing lake shrinkage-diversity relationships are not readily

available, in part because plant diversity is a lower management priority than the maintenance of wildlife populations and their habitat (USFWS, 1987).

Plant traits, such as woodiness, relative growth rate, and specific leaf area, can regulate ecosystem properties such as C storage, primary productivity, and resilience to disturbance (Díaz et al. 2007; Cadotte et al. 2011). This aspect of diversity can be captured by characterizing plant communities in terms of functional diversity, which is the distribution of functionally important species and traits (Tilman 2001; see Table 2.1 for examples of functional traits). Functional diversity encompasses three components: (1) the relative abundance of individual traits (functional composition), (2) variation in trait values within a plant community (functional divergence, sometimes referred to as functional diversity in other studies; Mason et al. 2005), and (3) the relative abundance of 'idiosyncratic species' that possess unique trait assemblages and may have effects on ecosystem function disproportionate to their abundance (Conti and Díaz, 2013).

Representing the functional diversity of plant communities may be an effective way to improve predictions of boreal C storage under changing disturbance regimes (Jonsson and Wardle 2010). Wildfires can remove C stored in soils and plant biomass, and reduced soil moisture (due to fire-induced lake shrinkage or permafrost loss) could accelerate decomposition of soil organic matter and reduce the potential for it to re-accumulate (Schimel et al. 2011). However, C cycling may also be related to plant functional traits (De Deyn et al. 2008; Conti and Díaz 2013). For example, plant growth and biomass production rates affect soil organic matter accumulation, while woodiness and tissue nutrient concentration regulate litter decomposition (De Deyn et al. 2008). In addition, plant traits can moderate the effects of disturbance on plant mortality and subsequent regrowth (Conti and Díaz 2013).

There are two primary hypotheses that link plant functional diversity (which I will refer to as 'functional diversity' hereafter) to C storage. According to the mass-balance hypothesis, ecosystem function is affected by the most abundant plant functional traits, or the assemblage of traits represented by the most abundant plant species (Grime 1998). This hypothesis predicts that functional composition (the relative abundance or frequency of occurrence of traits within a plant community) and idiosyncratic species effects (the relative abundance or frequency of occurrence of plant species within a community) should be the best predictors of organic C production and decomposition, and therefore of C storage (Díaz et al. 2007). In contrast, the niche complementarity hypothesis predicts that organic matter production and decomposition will be positively correlated with functional divergence, because resources will be distributed most efficiently among plant species with diverse ecological niches (Trenbeith 1975; Liang et al. 2015). For example, diverse rooting depth profiles could utilize more of the thawed soil profile and increased total root biomass production (Steinbeiss et al. 2008).

The mass-balance hypothesis and the niche complementarity hypothesis represent alternative, but not mutually exclusive, mechanisms by which plant community composition could mediate the effects of disturbance on above- and below-ground C storage. Relative support for the mass-balance hypothesis and the niche complementarity hypothesis can be assessed in terms of statistical support for correlations between C stock measurements and 1) variables that represent functional composition and idiosyncratic species effects or 2) variables that represent functional divergence. However, the three functional diversity components and their relationships with ecosystem function have rarely been examined in natural systems or at regional or greater spatial scales (Conti and Díaz 2013).

My objective was to evaluate whether functional diversity mediated the effects of lake shrinkage and wildfire on above- and below-ground C storage in boreal Alaskan wetlands, through the use of field data from a large-scale survey in the Yukon Flats National Wildlife Refuge, a 3.5 million ha wetland complex. I also examined how spatial patterns of C storage correlated with plant community characteristics that are relevant for wildlife habitat, because such relationships could be used to inform and re-evaluate management strategies for boreal lowlands in interior Alaska. I characterized wetland plant communities in terms of three components of functional diversity (functional composition, functional divergence, and idiosyncratic species) and their apparent effect on C storage. I then followed a published framework (Díaz et al. 2007), in which the effects of environmental forces and functional diversity components are assessed in three steps: 1) separate models for each component, 2) a combined model to assess relative importance, and 3) an investigation of nonlinear and interactive effects (referred to as 'discontinuous effects' in the referenced paper). Finally, I added to that work by developing a robust analytical approach for identifying non-linear and interactive relationships between functional diversity, disturbance, and above- and below-ground C storage using a combination of machine learning algorithms and structural equation modeling.

My analyses were based on a conceptual model of variation in lake-margin wetland C storage that incorporated two alternative hypotheses (Fig. 2.1): Hypothesis 1) Disturbance, including wildfire and lake shrinkage, directly altered lake-margin wetland C stocks through changes to the physical environment alone (i.e. combustion of organic C and changes to physical variables such as soil moisture, which can influence new biomass production, respiration, and decomposition). Hypothesis 2) Disturbance effects on above- and below-ground organic C stocks were mediated by changes in plant community structure and functional diversity (Fig. 2.1).

Within the framework of Hypothesis 2, my conceptual model included all three functional diversity components (functional composition, idiosyncratic species effects, and functional divergence) as potential predictors of C storage. Functional diversity variables were based on a suite of 10 functional traits associated with rates of organic matter accumulation and decomposition, and with plant community responses to changes in hydrology and fire history (Table 2.1). I also considered whether apparent effects of lake shrinkage on C stocks could be explained by the association of lake surface area trends with fire history (Fig. 2.1). All arrows in Fig. 2.1 represent hypothetical causal pathways between variables.

I used structural equation models (Grace et al. 2010) to test my conceptual model against data from two lake-margin wetland plant communities, Grass/Sedge (GS) and Deciduous Shrub (SH), as well as the adjacent upland forest community (F). I expected these three communities to reflect a gradient of increasing potential functional diversity. In terms of the overall relationship between disturbance (lake shrinkage and fire) and C storage, I predicted that lake shrinkage would lead to increased AGB in near-shore (GS) communities, with similar but weaker effects in the SH community, and no change in F biomass. I also predicted that lake shrinkage would result in increased decomposition and reduced soil organic C by reducing moisture in the formerly saturated and presumably anoxic soils of the GS community (Chapin et al. 2011; Chapin et al. 2009).

I predicted functional divergence and functional composition would both be positively correlated with fire frequency (Jonsson and Wardle 2010), but C storage would be negatively correlated with fire frequency, and that both patterns would be evident in all community types (Grosse et al. 2011). For functional diversity, I predicted that the relative importance of functional diversity as a mediator of disturbance effects and the relative support for the niche

complementarity hypothesis would both be highest in the F community, which had the most complex canopy structure and therefore the greatest potential for niche differentiation among plant species (Conti and Díaz, 2013; Liang et al. 2015).

Methods

Study Area

I chose the Yukon Flats National Wildlife Refuge (YFNWR) in northeastern Alaska as my study area. The YFNWR encompasses 3.5 million ha surrounding the Yukon River floodplain, consists of a complex mosaic of ~ 40,000 lakes, wetlands, and upland forest underlain by discontinuous permafrost (Gallant 1998; Roach et al. 2011). Lake shrinkage trends within the refuge span the full range of variation observed across the state (Roach et al. 2013). As is common in boreal lowlands, lakes are associated with concentric rings of herbaceous fens and woody wetlands dominated by *Salix* species (Whitehouse and Bayley 2005).

Plant species diversity sampling

I surveyed plant communities at 66 lakes between 2010 and 2011. I selected candidate focal lake sites from a GIS layer of floatplane-landable lakes using a Generalized Random Tessellation Stratified (GRTS) design, ensuring that my sample lakes were a spatially balanced, random sample of the study area (Stevens and Olsen 2004). All lakes within a 1-km radius of the focal lake centroid that could be accessed within 14 days were sampled as satellite lakes. This design allowed me to include small, unlandable lakes in my sample.

I established four perpendicular 100m survey transects at each lake, oriented at a random azimuth to the lake centroid. Each transect began at the lake edge, defined as the point where the soil surface was not covered by standing water. I recorded all vascular species located within 5m of the transect line, and pressed unidentified specimens for laboratory identification. I visually

estimated species percent cover using a 50 m x 100 m grid centered on a randomly selected transect and containing 25 uniformly distributed 5 m-radius vegetation plots. Finally, I delineated transitions between concentric rings of plant community types around each lake based on the plant growth form (herbaceous, deciduous shrub, or tree) with >50% cover. I used these measurements to generate buffers around each lake and estimate GS and SH community size in ArcMap 10.0. I also calculated F area within 100m of the lakeshore. GS and SH sizes represented the total size of the community surrounding each lake, and were used to account for diversity-area relationships that could have been correlated with or independent from disturbance history. F size values were largely an artifact of the 100m transect sampling design, but were nevertheless included in analyses because those artifacts could have been correlated with F plant diversity measurements, and could therefore have mediated apparent disturbance-diversity relationships.

Fire History

I estimated the time since the most recent fire at all sample lakes by overlaying lake locations with a GIS map of historical fire perimeters from 1950 to the present (fire.ak.blm.gov). Because only 1/3 of all sample sites had burned within that timeframe (n=35), I represented fire history as an ordinal variable: 1 = < 5 years since fire, 2 = < 10 years, 3 = < 25 years, 4 = < 50 years, and 5 >= 50 years.

Lake Trends

I estimated trends in lake surface area between 1986 and the present using linear models fit with a time series derived from a sequence of 22 Landsat satellite images (Rover et al. 2012). Models included Year and ordinal day of year to incorporate seasonal and inter-annual variation (Equation 2.1; Roach et al. 2011).

(2.1) $$Lake\ surface\ area\ = \beta_1 + \beta_2 * Year + \beta_3 * Day\ of\ Year$$

Lakes with significant model fit and significant negative Year coefficients ($\alpha = 0.05$) were characterized as shrinking (n=16, 12% of sample). This proportion was similar to the total proportion of shrinking lakes in the YFNWR (~10%; Rover et al. 2012). Three lakes had significant increasing trends, and were excluded. Increasing lakes represent a small fraction of the total landscape (<3%) in YFNWR and elsewhere in Alaska (Rover et al. 2012).

Soil C and AGB sampling

I sampled plant AGB as a measure of above-ground organic C storage (Ji et al. 2012), and used soil organic layer thickness (OLT) as a proxy for below-ground organic C (Johnson et al. 2011). I visited six stable and four shrinking lakes either in 2010 or 2012 between Aug 1 and Aug 14, which corresponded to peak biomass (Mack et al. 2008). Within each community type (GS, SH, and F), I harvested all live and dead understory AGB from 5-10 randomly located 20cm x 50cm quadrats. Samples were kept cool and frozen within 3 days. I then dried samples for 3 days at 60° C before weighing (Shaver and Chapin 1991; Mack et al. 2008). I also measured shrub (<3m tall) stem density along a randomly located 5m-wide, 60m-long transect in each community, broken into six 10m cells, and harvested 10 stems per community type to estimate biomass per stem. All stem material was dried for 5 days at 60° C before being weighed. I estimated tree density in each cell using a third nearest neighbor angle-order estimator (Engeman et al. 1994; Sheil et al. 2003), and calculated tree biomass using allometric equations (Bond-Lamberty et al. 2002; Yarie and Kane 2007). Total AGB was calculated by summing understory, shrub and tree AGB per m^2.

I collected three 20cm soil cores from each plant community using a 4.8 cm diameter circular fitting for a Makita power drill, which minimized compression in organic horizons.

Horizon depths and weights were recorded in the field, and samples were kept cool and frozen at -20° C within 3 days. I dried samples at 60° C in the lab before measuring % C and N with a Costech CHN analyzer. Bulk density was estimated using a known-volume subsample for each horizon in each core. I then calculated soil C content per m^2 (Equation 2.2; Johnson et al. 2011)

(2.2) $$g\ C * m^{-2} = \%C * bulk\ density * layer\ thickness\ (cm) * (5.76\ cm^2 * 0.0001)$$

I also characterized soil horizons at all 66 vegetation-sampling lakes in pits dug along the four vegetation survey transects. Finally, I verified that soil OLT, which I measured at all lakes, could be used as a proxy for soil C content per unit area (Johnson et al. 2011), by developing a regression model predicting soil C content based on horizon type and thickness using data from the 10 lakes where soil cores were collected. OLT was used as the dependent variable representing soil organic C in subsequent analyses.

I compared mean field AGB estimates to Landsat-derived mapped estimates (Ji et al. 2012) for the buffer polygons representing each community type. Satellite-derived estimates were found to have a cross-validated accuracy of 73% when compared with field data, and were approximately unbiased with respect to field AGB (Ji et al. 2012). I conducted my own validation by regressing my field biomass estimates against mapped values, and used this regression model to extrapolate mean AGB for all communities at all 130 lakes.

Functional diversity and functional composition

I calculated plant functional trait diversity based on five effect traits and five response traits (Table 2.1). These traits were selected based on their potential to influence rates of organic C accumulation and decomposition, and on their relevance for predicting plant community responses to lake-related disturbance. I developed separate trait matrices for all species found in

each plant community, using a combination of field data, literature searches, and a query from the TRY functional trait meta-database (www.try-db.org; Kattge et al. 2011). I filled data gaps using multiple imputation, as implemented in the mice R package, after confirming that there was sufficient data (< 1/3 missing) to retain each functional trait variable (Taugourdeau et al. 2014).

I estimated functional trait divergence using Rao's quadratic entropy (Rao 1982), which is derived by calculating the multivariate distance between each species pair in a community, and weighting these distance scores by the proportional abundance of each species (Equation 2.3).

(2.3) $$\sum p_i * p_j * d_{ij}$$

p_i, p_j = proportional abundance of species i, j. D_{ij} = multivariate distance between species i, j.

Gower's distance formula was used to accommodate the presence of both continuous and categorical trait variables in my dataset (Roscher et al. 2012). Functional trait composition was estimated by 1) calculating the community-weighted mean (CWM) of functional trait values for all species present at a given lake and community type, and 2) extracting the first principal component score from a PCA of CWM functional trait values (Roscher et al. 2012). Community-weighted mean trait values were an average over all species present, weighted by species abundance.

I used the random forest algorithm to identify potential idiosyncratic species that were strong predictors of above- and below-ground C (Cutler et al. 2007). I ran separate random forest models for AGB and OLT in each community type, with binary presence/absence scores for all plant species as independent variables. Variables were ranked based on their average individual

effect on model mean squared error (Archer and Kimes 2008). Since the presence of many unimportant predictors can suppress model performance, I sequentially removed the 5 lowest-ranking variables and re-ran models until I arrived at a model with maximum predictive power (Strobl et al. 2007). Model results were used to construct reduced species presence matrices. I then calculated idiosyncratic species scores for each community and response variable as the first principal component of a species presence/absence PCA.

Structural equation modeling

I used structural equation modeling (SEM) to evaluate hypotheses about the network of causal relationships linking lake shrinkage, plant community traits, and C storage. The SEM modeling framework facilitates the testing of hypotheses about direct and indirect influences, and makes it possible to explicitly account for causal relationships between predictor variables (Grace and Anderson 2010). These features make SEM modeling a more appropriate tool for addressing my research questions than more common statistical techniques such as general linear models, in which unaccounted-for covariance between predictors can have a dramatic influence on parameter estimates (Grace et al. 2014)

My first step was to graphically represent *a priori* hypotheses about the network of causal relationships that might drive variation in AGB and OLT, which reflect above- and below-ground C respectively (Fig. 2.1). Concepts such as disturbance, functional diversity, and C storage were represented by measured variables (Table 2.1), producing a hypothetical network of influence that could be directly compared against data. A directed arrow from one variable to another (x -> y) represents the hypothesis that 'y is a linear function of x' (Fig. 2.1).

I fit this network to my data with the lavaan package in R using the LISREL method, and assessed model fit by comparing the observed variance-covariance structure of the data to a

modeled variance-covariance matrix using a Chi-squared test (Grace and Anderson 2010; Rosseel 2012). A significant test statistic implied inadequate model fit and missing structural relationships between variables, and was corrected by adding biologically plausible paths sequentially based on modification index values (Chaudhary et al. 2009). I assessed my hypotheses by examining the standardized path coefficients linking variables (Grace 2006). Finally, I also assessed the predictive power of my hypotheses by examining model R^2 values for each response variable.

Results

Overall, mean AGB within 100 m of a lake was highest in the GS community (mean=87.15 Mg/ha, SE=1.41) and lowest in the F community (mean=83.34, SE=0.81; Table 2.2). Values were averaged over all lakes, including those where a particular community type was absent within transect boundaries. GS also occurred most frequently within 100m of lakes, while the F community was least common. OLT was also greatest in the GS community (mean=28.2 cm, SE=1.2), whereas there was little difference between SH and F OLT (SH mean=19.5 cm, SE=1.2; F mean=18.6 cm, SE=1.1; Table 2.2). SH and GS Rao values were similar to each other, (SH mean = 15.58, SE=1.10; GS mean=14.62, SE=1.68), and both were higher than mean F Rao value (mean=7.99, SE=0.87; Table 2.2). The opposite pattern was observed for species richness: On average, species richness of vascular plants was higher in the upland forest than in GS or SH (F mean = 60.12, SE=4.40; GS mean=51.30, SE=3.82; SH mean=46.26, SE=3.94).

Bivariate relationships: Vegetation

Measured and satellite-derived AGB were significantly positively related, although the strength of this relationship ($R^2 = 0.58$; $p = 0.002$) was lower than the 73% accuracy reported by

Ji et al. (2012). AGB per unit area was significantly positively related to the length of time since the most recent wildfire in all three communities (Table 2.3). GS and SH communities adjacent to shrinking lakes also had significantly lower AGB per unit area compared to similar communities near stable lakes (Table 2.3). Size (width of community zones surrounding lakes) was the best single predictor of AGB per unit area in all communities, with R^2 values ranging from 0.33 to 0.54). Size was negatively associated with AGB per unit area in GS and SH communities, but was positively correlated with biomass in the F (Table 2.3). Lake shrinkage was not significantly associated with AGB per unit area in the F community (Table 2.3). Functional divergence (Rao's quadratic entropy) was significantly positively correlated with AGB per unit area in GS and SH communities, but not in the F. Functional composition, as measured by the first principal component score from a PCA of community-weighted mean (CWM) functional trait values, was not significantly associated with biomass in any plant community. The first principal component from a PCA of idiosyncratic plant species presence/absence was significantly correlated with AGB in all three communities (Id Spp; Table 2.3).

Bivariate Relationships: Soils

Soil organic C content per unit area was explained well by a regression model with organic soil horizon type and OLT as predictors (R^2=69.77; $p<0.0001$). OLT was significantly predicted by time since fire in the GS and SH communities, negatively correlated with Size in the F, and significantly correlated with idiosyncratic species scores in the SH and F communities (Table 2.3). Idiosyncratic species scores for SEM models of OLT were primarily associated with the presence of forb and graminoid species (Appendix A), although SH IdSpp scores were

positively correlated with the presence of one shrub species (*S. glauca*), and F IdSpp scores were positively correlated with the presence of one deciduous tree (*Populus tremuloides*; Appendix A)

Using random forest models of idiosyncratic species to predict above- and below-ground C

Random forest models using only community-weighted mean functional trait values were poor predictors of AGB (Table 2.4), but idiosyncratic species models explained 43% of variance in the GS community, 48% in the SH community, and 61% in the F. The optimal model for each community included 15 species, although the top five species accounted for over half the variance explained in all cases (% variance explained = 36 for GS, 29 for shrub, and 49 for the F. Species were grouped into six plant functional types (Table 2.5), which characterize growth form and are expected to represent species with broadly similarly functional traits (Chapin et al. 1996). The presence of the top-ranked idiosyncratic species was a significant predictor of AGB in all communities. For instance, *Chamerion angustifolium* (fireweed), a post-disturbance colonizing forb, was the top predictor of GS AGB (Table 2.5). GS communities where fireweed was present had significantly lower biomass than those where it was absent (present: mean=84.93 Mg/ha, SE=1.61, n=34; absent: mean=90.82 Mg/ha, SE=2.06, n=19; t=-2.25, df=38.82, p=0.03; Fig. 2.2). The top predictor in the SH community was the dwarf deciduous shrub *Arctostaphylos rubra*, and the best predictor of forest AGB was the forb *Galium boreale*, although a deciduous shrub (*Salix pseudomonticola*) and an evergreen shrub species were also highly ranked (*Linnaea borealis*; Table 2.5). In general, herbaceous species were more strongly associated with variation in AGB in the GS community, while woody plants had high variable importance values in the shrub and forest communities (Table 2.5).

OLT, like AGB, was not well predicted by community weighted mean functional trait values, with CWM random forest models explaining less than 1% of variance in OLT in the GS

and Shrub communities, and only 15% of variance in F OLT (Table 2.4). IdSpp random forest models were more successful, explaining between 40 and 57% of variance in OLT. All top predictors of GS OLT were herbaceous (graminoid or forb) species, including several plants found in emergent wetlands and floating vegetation mats, such as *Calla palustris* and *Menyanthes trifoliata* (Table 2.5). Deciduous tree and shrub species were generally not strong predictors of OLT in any community, although the nitrogen fixing shrub *Alnus viridis* had the second highest variable importance ranking of any species in the SH IdSpp model (Table 2.5). The only woody species with high variable importance rankings in the F model were understory evergreen shrubs (*Ledum palustre* and *Vaccinium oxycoccus*).

Structural equation modeling of Above-ground C storage (AGB)

In all communities, AGB was significantly associated with both disturbance history (time since fire, lake shrinkage status) and functional diversity variables (Rao and IdSpp). Structural equation models (SEM) explained more than half of observed variation in AGB in all communities (R^2= 0.6 for GS, 0.59 for SH, and 0.73 for F; Figure 2.3). All SEM models adequately captured the underlying variance-covariance structure in the data, as indicated by non-significant Chi-square tests (Figure 2).

Time since fire was positively correlated with AGB in all communities, although the relative strength of this effect was greatest in the GS community (Table 2.6). Only direct pathways linked fire history with AGB in the GS and F, while the effects of fire history were at least partially mediated by changes in functional diversity in SH (Fig. 2.3).

Lake shrinkage was significantly associated with increased AGB per unit area in both the GS and SH communities (Fig. 2.3). In both cases, effects of lake shrinkage on biomass did not

appear to be mediated by functional diversity. Lake shrinkage status was not significantly predicted by time since fire (Fig. 2.3).

Size was the strongest direct influence on AGB per unit area in the GS and SH communities (Fig. 2.3). Small/narrow GS and SH community zones surrounding lakes had higher mean biomass density relative to wider zones. Wetland size and AGB were positively correlated in the F, where measured size was limited by the 100m length of sampling transects. Strong positive relationships between size and idiosyncratic species effects in the F also indicated that sampling a wider section of the F communities surrounding lakes increased the likelihood of encountering idiosyncratic species with strong influences on biomass.

Idiosyncratic species effects were the only components of functional diversity with direct influence on AGB (Fig. 2.3). Idiosyncratic species scores were significantly positively correlated with Rao's quadratic entropy scores, which represent functional divergence, in the GS and SH communities (Fig. 2.3). In other words, species with a disproportionate apparent influence on AGB were more likely to occur in communities with high functional divergence. A similar but non-significant trend was produced in the F AGB SEM model (Fig. 2.3). Rao's quadratic entropy was not consistently predicted by any variable across the three communities, but increased with increasing time since fire in the SH (Fig. 2.3). Functional trait composition, as measured by CWM scores, was not strongly associated with biomass in any community (Fig. 2.3).

Peat thickness (OLT) structural equation model results

Structural equation models explained close to 30% of observed variance in OLT thickness in all three communities, representing approximately half the predictive power of AGB SEM models (Fig. 2.4). The influence of disturbance and functional diversity variables, and the evidence for mediation of disturbance effects by functional diversity varied between

communities. When direct and indirect pathways were included, OLT increased with time since fire in both the GS and SH communities, but not in the F (Fig. 2.4). In contrast, lake shrinkage was only associated with OLT in the SH. The effects of lake shrinkage on SH OLT included indirect pathways mediated by functional composition (CWM) and idiosyncratic species (IdSpp) effects, while Fire effects were mediated by Size, Rao, CWM, and IdSpp (Fig. 2.4).

Community size was not a significant predictor of GS OLT although it was positively correlated with OLT in both the SH and F via direct paths (Fig. 2.4). In the SH, this effect was countered by indirect pathways mediated by IdSpp and CWM, for a negligible net effect (Table 2.6).

The IdSpp variable was the strongest predictor of OLT in all communities, and was the only functional diversity variable linked to OLT via direct pathways (Fig. 2.4). Functional divergence (Rao) was only significantly correlated with OLT in the SH, with a net negative relationship (Table 2.6). In contrast with AGB SEM models, CWM was a significant predictor of SH and F OLT (Table 2.6). In both communities, the effect of CWM was positive and mediated by relationships between functional composition and idiosyncratic species effects (Fig. 2.4, Table 2.6). PCA results indicated that these positive CWM PCA scores were linked with the dominance of taller, woody, drought-tolerant species with the ability to re-sprout rapidly following disturbance (Fig. 2.5).

Discussion

Overview

I examined relationships between disturbance, functional diversity, and above- and below-ground C storage (AGB and OLT) in boreal lake-margin plant communities. I built on previously published methods (Díaz et al. 2007) by outlining an analytical framework for

simultaneously estimating the separate and interactive effects of functional diversity components on ecosystem function. I implemented this framework using plant diversity data from an intensive field survey across a 3.5 million-ha study area combined with an online plant trait database (Kattge et al. 2011), to test hypotheses about the ecological role of functional diversity in diverse, natural systems at a management-relevant scale.

Lake shrinkage was a significant mediator of AGB in lake-margin plant communities. I also found that the relative influence of functional divergence and functional composition differed between above-ground and below-ground C pools, and that correlations between functional divergence and AGB were at least partly mediated by correlations between AGB and idiosyncratic species effects. In addition to highlighting the power of idiosyncratic species analyses, my study also provided insight into the importance of patch size in functional diversity-ecosystem function analysis. I conclude by discussing how my work could help improve representation of plant biodiversity and disturbance in ecosystem models designed to predict high-latitude C dynamics, and by reviewing the implications of my work for land managers tasked with preserving the ecological and social value of boreal wetlands in a drying landscape.

Disturbance effects on C storage

My findings supported the hypothesis that lake shrinkage was a significant influence on C storage in lake-margin plant communities of interior Alaska. GS and SH wetlands near shrinking lakes had significantly increased AGB per unit area relative to areas with stable lakes, while drying SH communities had significantly thicker soil organic layers (Table 2.3). Although lakes within fire scars from the past 60 years were more likely to shrink than unburned lakes (Roach et al. 2013); the probability of shrinking was not related to time since fire over more recent time scales (Fig. 2.3, Fig. 2.4). In addition, lake shrinkage appeared to represent a distinct

form of disturbance whose influence on C stocks could not be explained as an indirect effect of increased fire frequency (Fig. 2.3, Fig. 2.4). As predicted, the effects of lake shrinkage were most apparent in communities close to the lakeshore (Table 2.6). Overall, lake shrinkage was more tightly linked to AGB than to the larger C stocks stored in organic soil (Fig. 2.3, Fig. 2.4). Lake shrinkage trends can only be calculated over a few decades (Roach et al. 2011; Rover et al. 2012), and this timespan may not be sufficient to show the effects of lake shrinkage on soil peat accumulation.

In addition to being a poor predictor of below-ground C, lake shrinkage was a relatively minor component of the local disturbance regime, with fire history being a stronger predictor of both above- and below-ground C stocks (Table 2.6). Wildfire is widely recognized as the dominant disturbance agent in interior Alaska (Harden et al. 2000; Balshi et al. 2007) and the Yukon Flats has experienced extensive wildfire activity in recent decades (Kelly et al. 2013). Surprisingly, the only C pool that was not significantly associated with time since fire in my analysis was the F organic layer. The effects of wildfire on OLT in the boreal forest are well established (Harden et al. 2000). However, my analysis used a relatively coarse measure of fire history that did not include estimates of severity or timing, both of which regulate the amount of surface organic material removed during boreal forest fires (Kasischke and Johnstone 2005; Genet et al. 2013). In addition, the F community included a spectrum of forest types with divergent soil profiles and drainage conditions, which have been shown to alter fire effects on post-fire vegetation and soil organic matter (Harden et al. 2000). Forest types in the study area included poorly drained pure black spruce stands (mean OLT = 18.84 cm) as well as drier mixed aspen-birch forests (mean OLT = 8.85 cm). This diversity in soil profiles among upland forest types, which has been documented throughout the Yukon River Basin (Pastick et al. 2014), may

have accounted for the significant pathways linking functional diversity and forest OLT (Fig. 2.4). However, if future fires increase in frequency and severity, fire history may become an increasingly important predictor of vegetation type and soil organic C (Johnstone et al. 2010).

C storage/community size relationships

Community size was one of the strongest predictors of both above and below-ground C in my analyses (Table 2.6). These effects could not be explained entirely in terms of size-diversity relationships, since direct pathways between community size and AGB/OLT were generally stronger than indirect, functional diversity-mediated pathways (Table 2.6). Furthermore, where community size-diversity relationships were detected, the sign was negative (Table 2.6; Whittaker and Triantis, 2012). I suggest this negative relationship, and the negative relationship observed between community size and AGB in both GS and SH communities (Fig. 2.3), can be explained as edge effects. As already noted, SH communities in the Yukon Flats are often characterized by infilling of both GS and F plant species. Similarly, the outer edges of GS communities typically contained shrub propagules and spruce or aspen seedlings. In both cases, these edge species had high idiosyncratic species scores, e.g., a tree *Populus tremuloides* and a deciduous shrub *Salix bebbiana* in the GS community (Table 2.5). My findings illustrate the need to explicitly consider patch size and spatial structure in analysis of functional diversity-ecosystem function relationships (Whittaker and Triantis, 2012).

Functional diversity mediation

The mediation hypothesis, which predicts that disturbance effects are mediated by changes in plant community structure and the distribution of functional characteristics, was not well-supported because significant indirect pathways linking disturbance to C storage were only detected in the SH community (Fig. 2.3, Fig. 2.4). This result was consistent with my prediction

that the importance of functional diversity as a mediator of disturbance effects would be positively correlated with mean functional divergence. Mean functional divergence varied significantly across plant communities and was highest in the SH community ($F_{2,157} = 10.1$, $p < 0.0001$; Table 2.2). This association was probably due to the variety of woody and non-woody growth forms present in the SH community, which was a zone of transition between herbaceous fens and upland forest (Whitehouse and Bayley 2005).

Of the two disturbance types I examined, the mediation hypothesis was only supported for fire history (Fig. 2.3, Fig. 2.4). Lake shrinking was not significantly correlated with any functional diversity variable in any community except for SH OLT functional composition scores (CWM). Interaction between shrinkage trends and functional diversity, particularly functional divergence, was apparently not related to species diversity; GS communities near shrinking and stable lakes had similar functional divergence levels, despite an average of 40% greater species richness at shrinking lake sites (Table 2.2). This discrepancy underscores the need to consider the influence of functional traits, rather than species diversity alone (Mayfield et al. 2010), when examining disturbance-diversity relationships.

Functional diversity hypotheses

My results provided support for the niche-complementarity hypothesis for AGB and the mass-balance hypothesis for OLT. (Sandra and Cabido, 2001). AGB increased with functional divergence scores (Rao's quadratic entropy) in all communities (Table 2.6). The standard explanation for this pattern, according to the niche complementarity hypothesis, is that a diverse array of functional niches allowed plant communities to use resources more efficiently (Díaz et al. 2007). However, in my study correlations between functional divergence and AGB were

explained mainly by the fact that communities with high functional trait divergence were more likely to contain individual species that were significantly associated with total biomass (idiosyncratic species effects; Díaz et al. 2007). Unlike AGB, soil OLT was associated with the abundance of functional traits, especially those characterizing woody vegetation (woodiness, plant height, leaf dry matter content; Fig. 2.5). However, similarly to my biomass results, the pathways linking CWM to OLT were mediated by idiosyncratic species effects. I interpreted this relationship to mean that the disproportionate effects of particular species on OLT can be associated with individual traits, specifically those traits that regulate the decomposability and lability of dead plant organic matter (Steinbeiss et al. 2008; Conti and Díaz, 2013). Overall, statistical evidence of idiosyncratic species effects can be interpreted as support for the mass-balance hypothesis (the idea that the dominance/presence of specific traits or species can influence ecosystem function; Díaz et al. 2007).

My results highlighted the importance of idiosyncratic species effects as the dominant functional diversity component. Under the functional diversity component framework I adopted, idiosyncratic species effects do not indicate a specific causal mechanism (Díaz et al. 2007). Apparent idiosyncratic species effects could be driven by associations between species and functional traits excluded from the analysis, or could reflect interaction between the unique combination of functional traits represented by a species and the environmental context in which those traits operate (Díaz et al. 2007; Eviner and Chapin 2003). As an example, unmeasured functional traits and trait interactions could explain the strong negative correlation between fireweed presence and GS above-ground biomass. Fireweed is a common plant in the region, and is one of the first to colonize burned or recently disturbed bare soil (Hultén 1968). Once established via wind dispersal, it can spread rapidly and quickly make up a substantial fraction of

understory biomass (Chapin et al. 2006; Hultén 1968). In addition, fireweed is similar in vegetative height (a trait included in my analysis) when compared to most common grass and sedge species (e.g. *Calamagrostis canadensis* and *Carex aquatilis*). As a result, the negative correlation between fireweed and AGB seems counterintuitive at first glance. However, fireweed has a simple, single-stemmed growth form, whereas many local grass and sedge species grow in closely spaced clumps or tussocks that could allow substantially higher density (Hultén 1968). As a result, the relationship between fireweed and total biomass may be explainable as a function of traits I considered (post-disturbance colonizing, growth rate), those I did not consider (growth form and horizontal density), and environmental context (seed availability, soil conditions). Additional experimental work is needed to confirm the causal relationship between fireweed and biomass, but my results nevertheless show that including idiosyncratic species effects can significantly increase the predictive power of functional diversity-ecosystem models, while also aiding the development of new hypotheses to guide future research.

Improving representation of functional diversity in ecosystem models

Although many existing ecosystem models incorporate functional diversity effects on ecosystem properties, they typically rely on coarse characterizations of functional diversity, such as plant functional types. My study is one of several recent examples demonstrating the need to account for trait-level diversity and idiosyncratic species effects, particularly when modeling ecosystem responses to disturbance (Jonsson and Wardle 2010), and there is growing interest in the development of ecosystem models that capture these effects (Wullschleger et al. 2014). Empirical models linking plant traits to ecosystem function can help to inform models with dynamic vegetation components in several ways. First, trait-based analyses can improve the delineation of plant functional types by revealing when functional types correspond to the

distribution of functional traits among species (Wright et al. 2006). Second, empirical trait-level analyses can potentially inform data collection for model parameterization, by highlighting idiosyncratic species (e.g. fireweed in the nearshore GS community) for targeted measurement of functional traits (Wullschleger et al. 2014). Finally, estimates of the responses of functional diversity metrics and trait values to changing environmental conditions could be used as targets for model validation (Soranno et al. 2010). It is essential to understand these relationships in order to develop models in which functional traits are allowed to change dynamically, thereby allowing models to effectively capture the role that high-latitude plant communities play in regulating some of the largest C stocks on the planet.

Management Implications and Conclusions

In the context of land management, two take-home messages emerged from this study. First, although lake shrinkage affects organic C sequestration and other functional values provided by boreal wetland ecosystems, the landscape-scale significance of these effects can be overshadowed by other landscape characteristics. Specifically, fire history as well as the diversity and composition of local plant communities were stronger predictors of above- and below-ground C than shrinkage trends in lake-margin plant communities. Second, although plant diversity has historically been a low management priority in lowland boreal Alaskan landscapes (USFWS 1987), the functional diversity of plant communities in these landscapes appears to influence valuable ecosystem functions. In addition to C sequestration, plant functional traits (woodiness, tissue nutrient concentrations, etc.) affect wildlife habitat quality in terms of forage and cover availability, and can influence the type and diversity of wildlife that a landscape can support (Jefferies et al. 1994; Paragi et al. 2008; Moretti and Legg, 2009; Rittenhouse et al. 2012). However, as the discrepancies between my AGB and OLT models illustrate, ecosystem

properties such as C storage, plant diversity, and habitat quality do not all co-vary in space, and respond differently to changes in disturbance regime. If the goal of management is to maximize value across all these properties, heterogeneous landscapes containing both shrinking and stable lakes and a diverse range of disturbance histories may provide better value than homogeneous patches dominated by large, stable lakes and wetlands.

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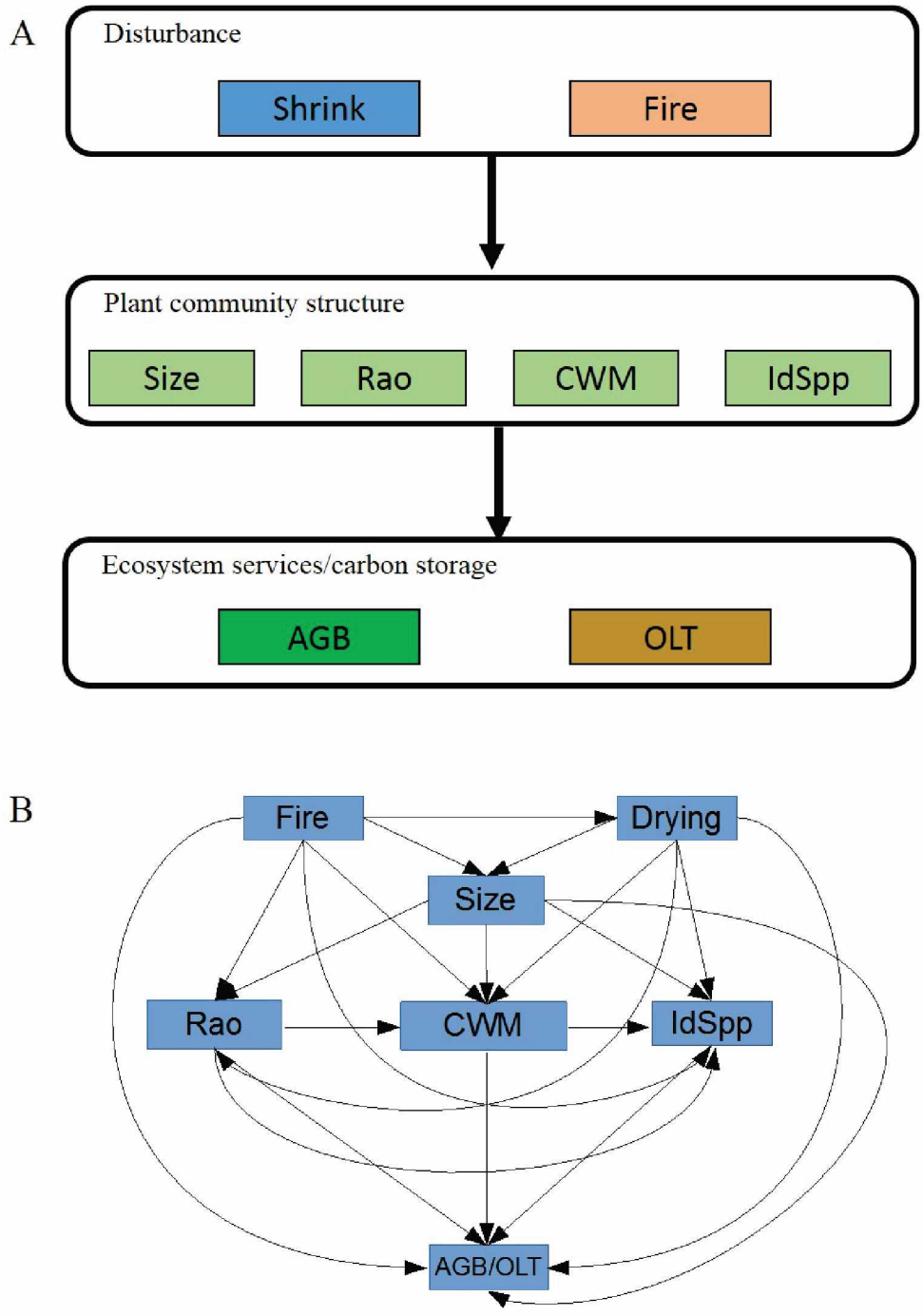

Figure 2.1. Functional diversity conceptual model. Panel A) general hypothesized direct and indirect linkages between disturbance, plant community structure, and carbon storage. Panel B) hypothesized relationships between all variables. Variables include shrinking trend (Shrink) time since fire (Fire), plant community zone width (Area), functional divergence (Rao), functional composition (CWM), idiosyncratic species effects (Id Spp), above-ground biomass (AGB) and organic layer thickness (OLT).

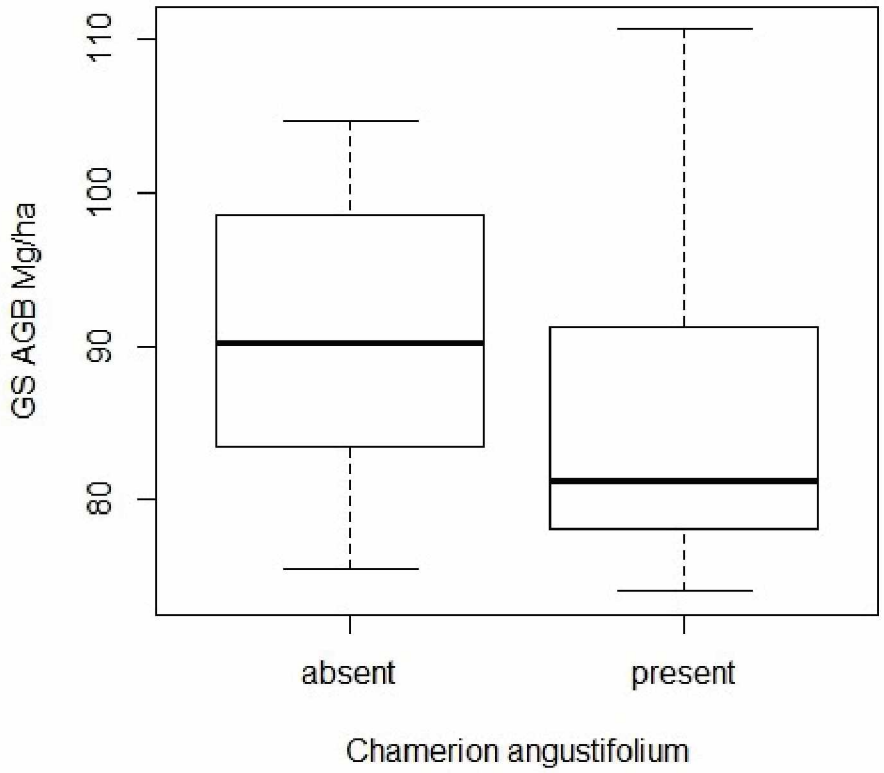

Figure 2.2. AGB as a function of fireweed presence. Boxplots of Above-ground biomass (AGB) in Grass/Sedge (GS) lake-margin plant communities where fireweed (Chamerion angustifolium) was present (n=34) and absent (n=19). Chamerion angustifolium was identified as an idiosyncratic species with the highest variable importance score in a random forest model predicting GS AGB as a function of vascular plant species composition. Biomass was significantly lower at lakes with fireweed than at those without it ($t = -2.25$, $df = 38.82$, p-value = 0.03).

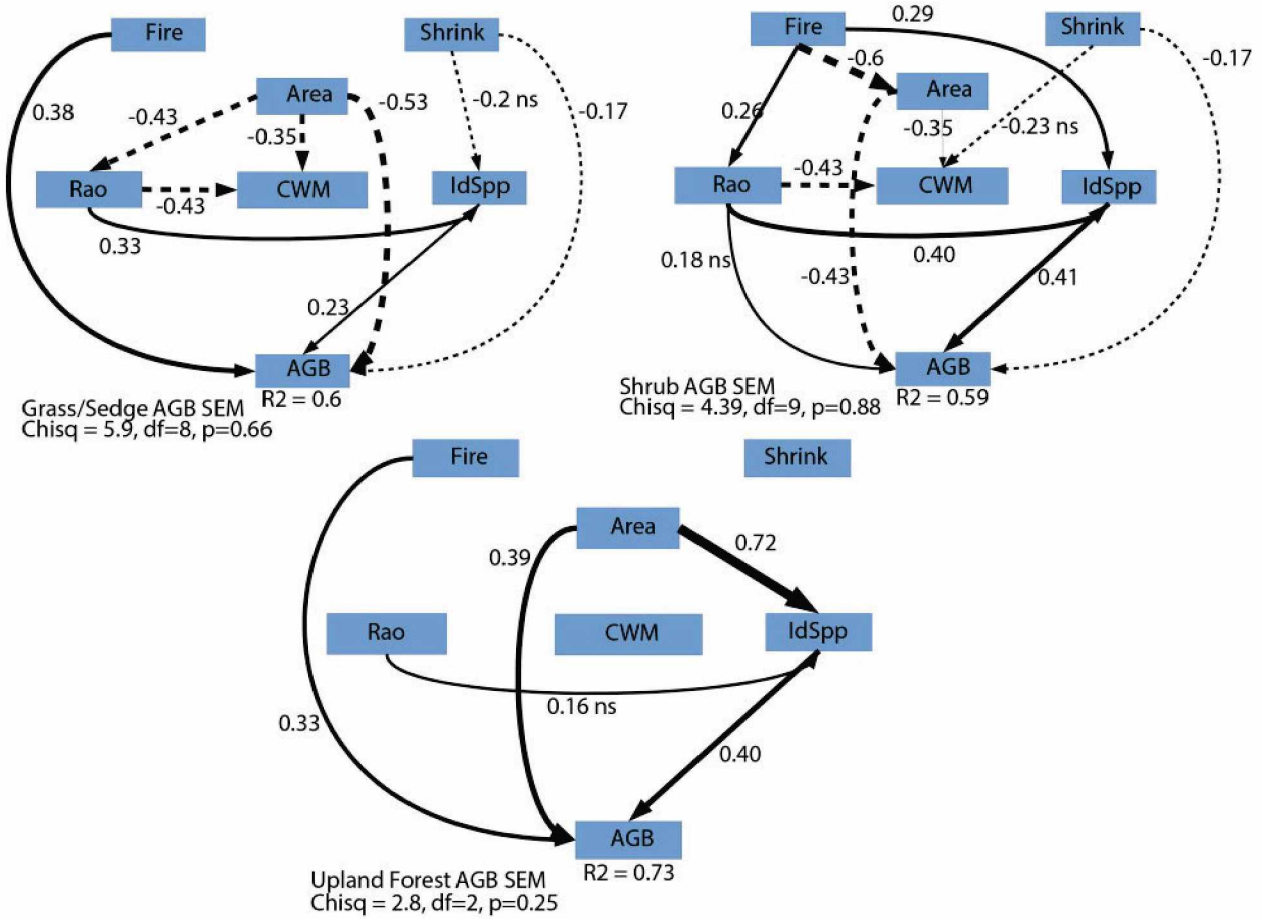

Figure 2.3. AGB structural equation model results. Path diagrams for structural equation models of relationships between shrinking trend (Shrink), time since fire (Fire), plant community zone width (Size), functional divergence (Rao), functional composition (CWM), idiosyncratic species effects (Id Spp), and above-ground biomass (AGB) in three plant communities: Grass/Sedge, Deciduous Shrub, and Upland Forest. Model variables are shown in boxes. Arrows indicate a linear causal pathway between two variables (Fire -> AGB implies that time since fire is a linear predictor of organic layer thickness). Solid arrows represent positive relationships, and dashed lines represent negative relationships. Standardized path coefficients in standard deviation units are shown for each pathway. Overall model fit was assessed with a Chi-Squared test. Non-significant test results indicate adequate model fit.

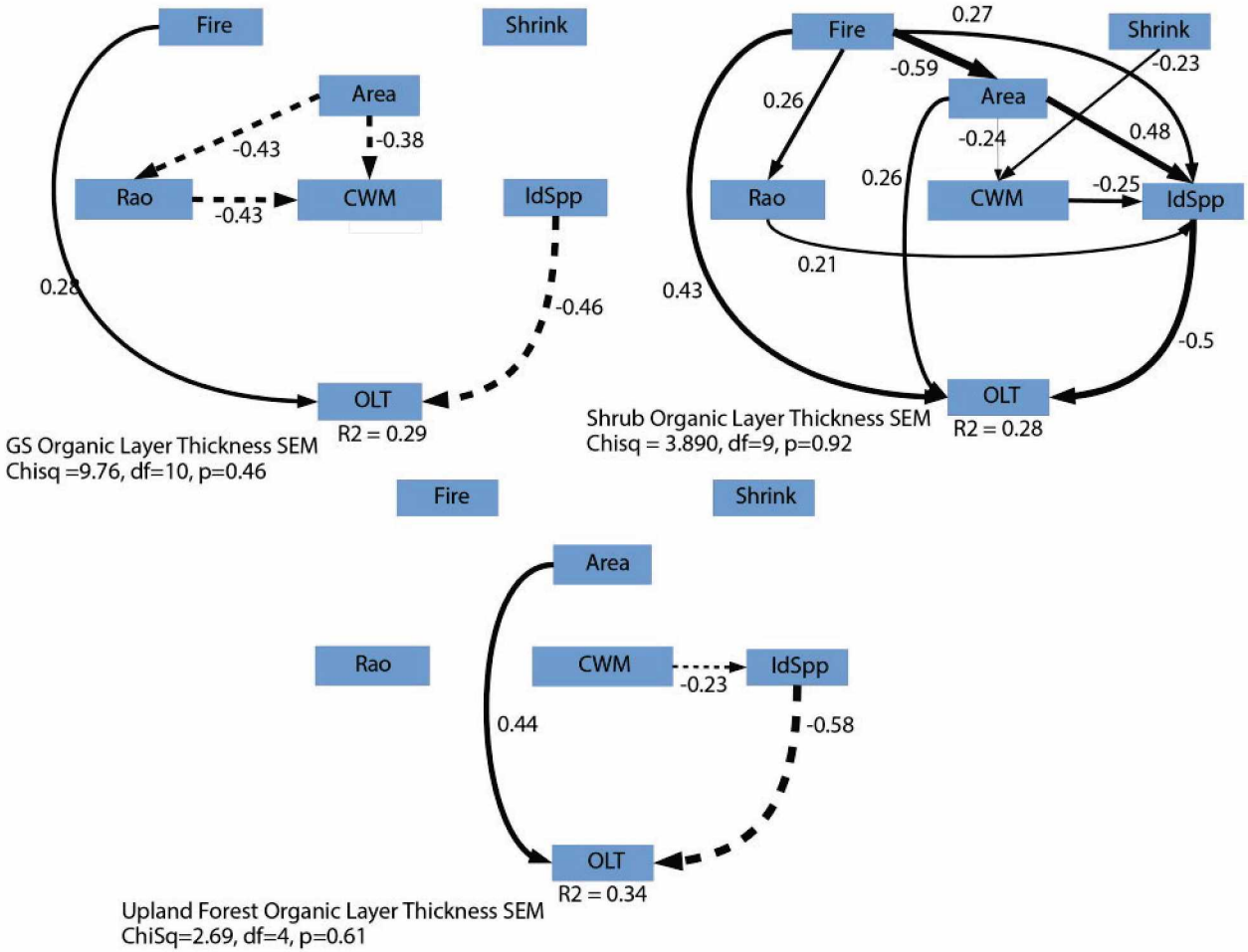

Figure 2.4. OLT structural equation model results. Path diagrams for structural equation models of relationships between shrinking trend presence (Shrink), time since fire (Fire), plant community zone width (Size), functional divergence (Rao), functional composition (CWM), idiosyncratic species effects (Id Spp), and organic layer thickness (OLT) in three plant communities: Grass/Sedge, Deciduous Shrub, and Upland Forest. Model variables are shown in boxes. Arrows indicate a linear causal pathway between two variables (Fire → OLT implies that time since fire is a linear predictor of organic layer thickness). Solid arrows represent positive relationships, and dashed lines represent negative relationships. Standardized path coefficients are shown for each pathway. Overall model t was assessed with a Chi-Squared test. Non-significant test results indicate adequate model fit.

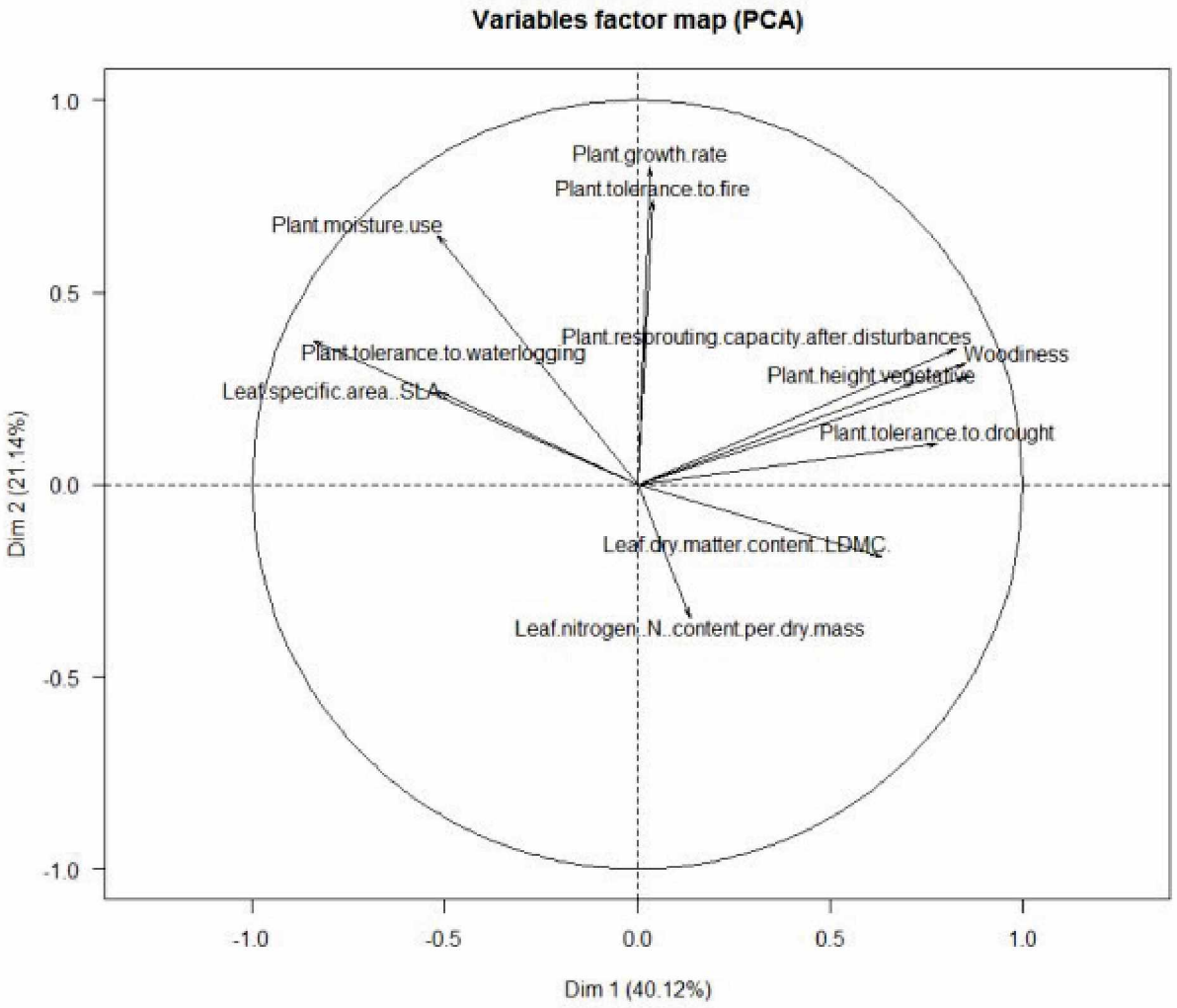

Figure 2.5. CWM functional trait PCA. Results of a principal component analysis of community-weighted mean functional trait values for Grass/Sedge communities adjacent to lakes in the Yukon Flats National Wildlife Refuge. PCA results for Deciduous Shrub and Upland Forest communities showed similar associations between traits and axes. Axes indicate the strength of correlation between measured variables and the first (horizontal) and second (vertical) principal component scores. The horizontal and vertical locations of arrow tips indicate correlation scores for each variable. Closely-grouped arrows indicate sets of functional traits that co-vary across lakes. The first (horizontal) axis corresponds to a suit of four traits that primarily characterizes deciduous shrubs, including woodiness, rapid re-growth following disturbance, and tolerance to relatively dry conditions in the Yukon Flats floodplain.

Table 2.1. Variable names and descriptions. A complete list of variables for A) Plant communities used in analyses, B) Functional trait variables used in calculation of functional divergence (Rao) and functional composition (CWM) scores, and C) variables used in structural equation models of disturbance, functional diversity and C storage.

A

Plant Community	**Abbreviation**	**Position**
Grass/Sedge	GS	1 (closest to lake)
Deciduous Shrub	SH	2 (intermediate)
Upland Forest	F	3 (farthest)

B

Functional Trait Name	**Data type**	**Effect/Response**	**Units**
Specific leaf area	continuous	Effect	cm2/g biomass
Leaf dry matter content	continuous	Effect	g dry mass / g wet mass
Leaf nitrogen content	continuous	Effect	%
Vegetative height	continuous	Effect	m
Woodiness	binary	Effect	
Tolerance to fire	ordinal	Response	0 (low) - 3 (high)
Tolerance to drought	ordinal	Response	0 (low) - 3 (high)
Tolerance to flooding	ordinal	Response	0 (low) - 3 (high)
Moisture use	ordinal	Response	0 (low) - 3 (high)
Re-sprouting capacity post-disturbance	ordinal	Response	0 (low) - 3 (high)

C

Variable	**Data type**	**Abbreviation**	**Units**
Time since fire	ordinal	Fire	0-10 years, 10-25, 25-50, >50
Lake shrinking trend	binary	Shrink	1= shrinking, 0 = stable
Community zone width	continuous	Size	m
Functional divergence score	continuous	Rao	none.
Functional composition score	continuous	CWM	none. 1st axis of CWM PCA
Idiosyncratic species score	continuous	IdSpp	none. 1st axis of IdSpp species PCA
Above-ground biomass	continuous	AGB	Mg/ha
Organic layer thickness	continuous	OLT	dm

Table 2.2. Lake-margin community characteristics. Means and standard errors for above- and below-ground characteristics of lake-margin plant communities in the Yukon Flats National Wildlife Refuge, contrasted by lake type (all, shrinking, stable). Variables are above-ground biomass (AGB; Mg/ha), organic layer thickness (OLT; dm), vascular species richness (Rich), functional divergence (Rao), functional trait community-weighted mean scores (CWM), and idiosyncratic species scores (IdSpp). Plant communities are grass/sedge (GS), deciduous shrub (SH), and upland forest (F).

Community	Variable	All lakes	SE	Shrinking	SE	Stable	SE	t (shrink vs. stable)	p (shrink vs. stable)
GS	AGB	87.15	1.41	87.73	3.52	86.09	1.52	-0.46	0.65
	OLT	2.82	0.12	3.60	0.19	2.80	0.13	-2.78	0.01
	Rich	51.30	3.82	67.14	11.08	48.18	4.82	-1.68	0.10
	Rao	14.62	1.68	18.85	6.48	13.43	2.06	-1.04	0.31
	CWM	-0.97	2.49	-6.51	5.11	-0.29	3.17	0.88	0.38
	IdSpp	0.02	0.08	-0.04	0.16	0.09	0.08	0.67	0.51
SH	AGB	84.01	1.12	83.61	2.27	83.88	1.37	0.10	0.92
	OLT	1.95	0.12	2.65	0.35	1.84	0.13	-2.64	0.01
	Rich	46.26	3.94	45.50	5.52	39.63	4.31	-0.70	0.49
	Rao	15.58	1.10	19.09	3.59	14.02	1.05	-1.87	0.07
	CWM	0.51	2.60	6.42	5.63	2.49	3.55	-0.55	0.58
	IdSpp	-0.01	0.08	0.18	0.16	-0.14	0.10	-1.63	0.11
F	AGB	83.34	0.81	83.40	1.64	82.88	1.14	-0.23	0.82
	OLT	1.86	0.11	0.99	0.31	1.20	0.12	0.73	0.47
	Rich	60.12	4.40	57.22	12.55	62.72	6.07	0.43	0.67
	Rao	7.99	0.87	6.40	1.57	7.80	1.26	0.58	0.57
	CWM	-0.26	2.57	-7.94	5.34	-0.97	3.36	1.03	0.31
	IdSpp	0.05	0.10	0.14	0.26	-0.03	0.15	-0.56	0.58

Table 2.3. AGB and OLT linear model results. Results from bivariate linear models predicting above-ground biomass (AGB) and soil organic layer thickness (OLT) using variables that describe disturbance history and functional diversity components, by plant community type. Community types are Grass/Sedge (GS), deciduous shrub (SH), and upland forest (F). Predictor variables are ordinal time since fire, annual trend in lake surface area (lake shrinkage), current wetland surface area (Area), functional divergence (Rao), community weighted mean functional trait values (CWM), and idiosyncratic species scores (Id.Spp).

		GS*			SH*			F*		
Response Variable*	**Predictor***	**R^2**	**slope**	**p**	**R^2**	**slope**	**p**	**R^2**	**slope**	**p**
AGB	Time since fire	0.16	3.57	0	0.22	3.41	0	0.22	3.17	0
	Lake shrinkage	0.11	-7.77	0.02	0.08	-5.61	0.03	0.02	-2.15	0.28
	Area	0.33	-0.24	0	0.28	-0.18	0	0.54	0.14	0
	Rao	0.13	0.31	0.01	0.19	0.44	0	0	-0.04	0.76
	CWM	0	0.02	0.83	0	0.03	0.61	0	0.01	0.74
	Id.Spp	0.19	5.82	0	0.17	7.6	0	0.47	4.53	0
OLT	Time since fire	0.07	0.21	0.05	0.07	0.21	0.05	0.02	-0.1	0.37
	Lake shrinkage	0	0.06	0.84	0.02	0.27	0.36	0	-0.03	0.9
	Area	0.06	-0.01	0.07	0.03	-0.01	0.21	0.15	-0.01	0
	Rao	0.02	0.01	0.36	0	0	0.76	0	0.01	0.7
	CWM	0	0	0.81	0.01	0.01	0.43	0.01	0	0.46
	Id.Spp	0	-0.06	0.96	0	-0.56	0.74	0.27	-0.47	0

Table 2.4. Random Forest model % variance explained. Model performance (% variance explained) for random forest models of above-ground biomass (AGB) and organic layer thickness (OLT) in three lake-margin plant communities (see Table 2.1), using idiosyncratic species presence/absence (IdSpp) and functional trait community weighted mean values (CWM).

		Model Type	
Response	Community	Id Spp	CWM
AGB	GS	43.36	0
	SH	47.71	14.59
	F	61.22	3.31
OLT	GS	56.59	0
	SH	38.65	0
	F	56.45	15

Table 2.5. Random Forest variable importance scores. Variable importance scores from random forest models predicting above-ground biomass (AGB) and soil organic layer thickness (OLT) based on the presence/absence of vascular plant species, by plant community (GS, SH, and F). Variable and community names are explained in Table 2.1. Species are grouped into one of six plant functional types which are expected to be broadly similar in growth form and functional traits. All species shown ranked in the top five variable importance scores for at least one community.

		AGB			OLT		
Plant Functional Type	**Species**	**GS**	**SH**	**F**	**GS**	**SH**	**F**
Deciduous tree	Populus tremuloides	4.45	8.22				
Deciduous shrub	Arctostaphylos rubra		23.9				
Deciduous shrub	Salix bebbiana	4.81	9.7				
Deciduous shrub	Salix pseudomyrsinites			13.03			
Deciduous shrub	Alnus viridis					12.3	
Evergreen shrub	Linea borealis			12.54			
Evergreen shrub	Ledum palustre						10.51
Evergreen shrub	Vaccinium oxycoccos						8.43
Equisetum	Equisetum scirpoides			10.51			9.02
Forb	Chamerion angustifolium	18.86		8.98			
Forb	Calla palustris	12.46					
Forb	Epilobium ciliatum	8.05					
Forb	Ranunculus sceleratus	7.73			10.33		
Forb	Cicuta virosa		9.04				
Forb	Eriophorum vagitum		7.55				
Forb	Galium boreale			13.13	11.11	18	5.64
Forb	Chenopodium rubrum				15.68		
Forb	Bidens cernua				10.54		
Forb	Caltha palustris				10.26		
Forb	Rubus arcticus					8.52	
Forb	Geum aleppicum					6.81	
Forb	Mertensia paniculata						11.02
Graminoid	Scolochloa festucacea	7.51					
Graminoid	Carex concinna			12.48		5.1	8.45
Graminoid	Carex sp					6.78	

Table 2.6. AGB and OLT structural equation model path coefficients. Summary of direct and indirect structural equation model path coefficients for structural equation models of above-ground biomass (AGB) and organic layer thickness (OLT), by plant community. Variable and community abbreviations are explained in Table 2.1. Indirect influence is the product of all path-coefficients for a multi-segment path linking two variables. Direct influence is the coefficient for a direct path between a single predictor and a single response.

Community†	Response†	Predictor	Indirect Influence	Direct Influence	Total Influence	Mediating Variables†
GS	AGB	Fire	0.00	0.38	0.38	
		Shrink	-0.05	-0.17	-0.22	Idspp
		Size	-0.03	-0.53	-0.56	Rao, Idspp
		Rao	0.08	0.00	0.08	Idspp
		Idspp	0.00	0.23	0.23	
	OLT	Fire	0.00	0.28	0.28	
		Idspp	0.00	-0.46	-0.46	
SH	AGB	Fire	1.05	0.00	1.05	Rao, Idspp, Area
		Shrink	0.00	-0.17	-0.17	
		Size	0.00	-0.43	-0.43	
		Rao	0.16	0.18	0.34	Idspp
		Idspp	0.00	0.41	0.41	
	OLT	Fire	-0.16	0.43	0.27	Area,Rao,CWM,Idspp
		Shrink	-0.03	0.00	-0.03	CWM,Idspp
		Size	-0.27	0.26	-0.01	CWM,Idspp
		Rao	-0.11	0.00	-0.11	Idspp
		CWM	0.13	0.00	0.13	Idspp
		Idspp	0.00	-0.50	-0.50	
Forest	AGB	Fire	0.00	0.33	0.33	
		Size	0.29	0.39	0.68	Idspp
		Rao	0.06	0.00	0.06	Idspp
		Idspp	0.00	0.40	0.40	
	OLT	Size	0.00	0.44	0.44	
		CWM	0.13	0.00	0.13	Idspp
		Idspp	0.00	-0.58	-0.58	

Appendix A. Idiosyncratic Species PCA results.

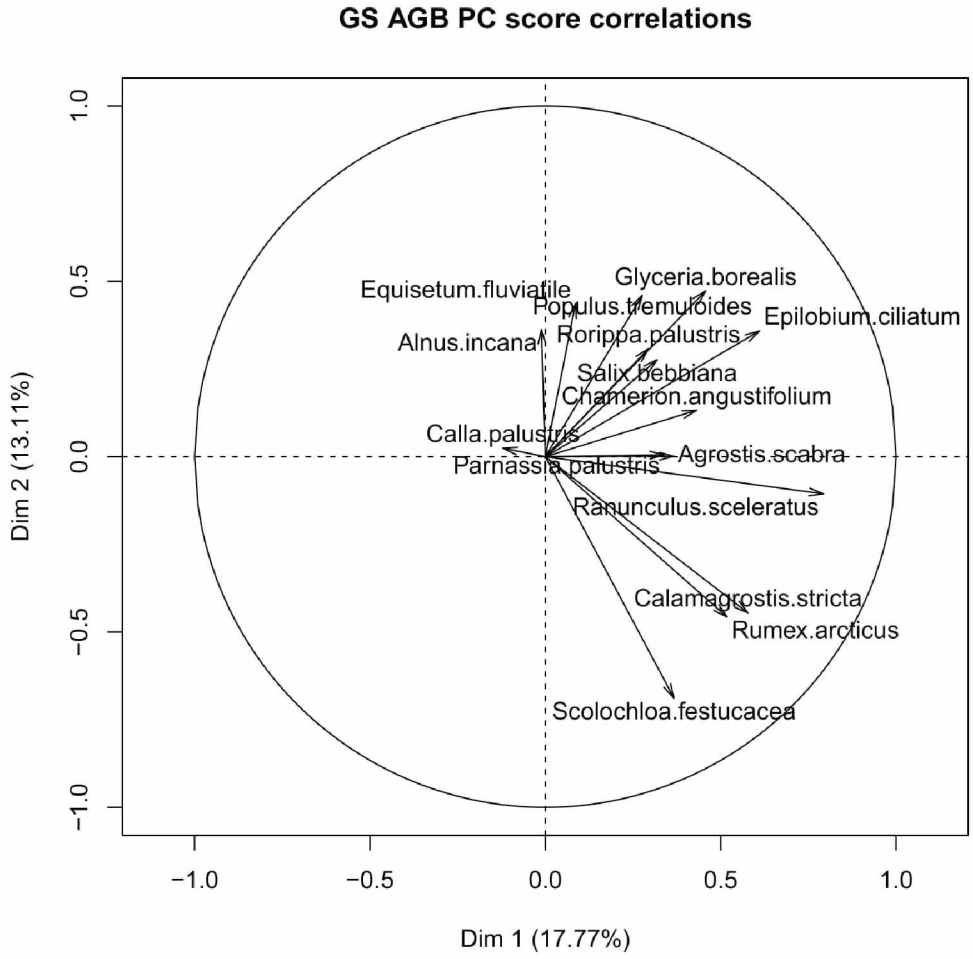

Figure A.1. Grass-Sedge (GS) community Principal Components Analysis. Arrows show correlations with individual above-ground biomass (AGB) idiosyncratic species abundance. Axis 1 scores were used as an index of idiosyncratic species presence/absence.

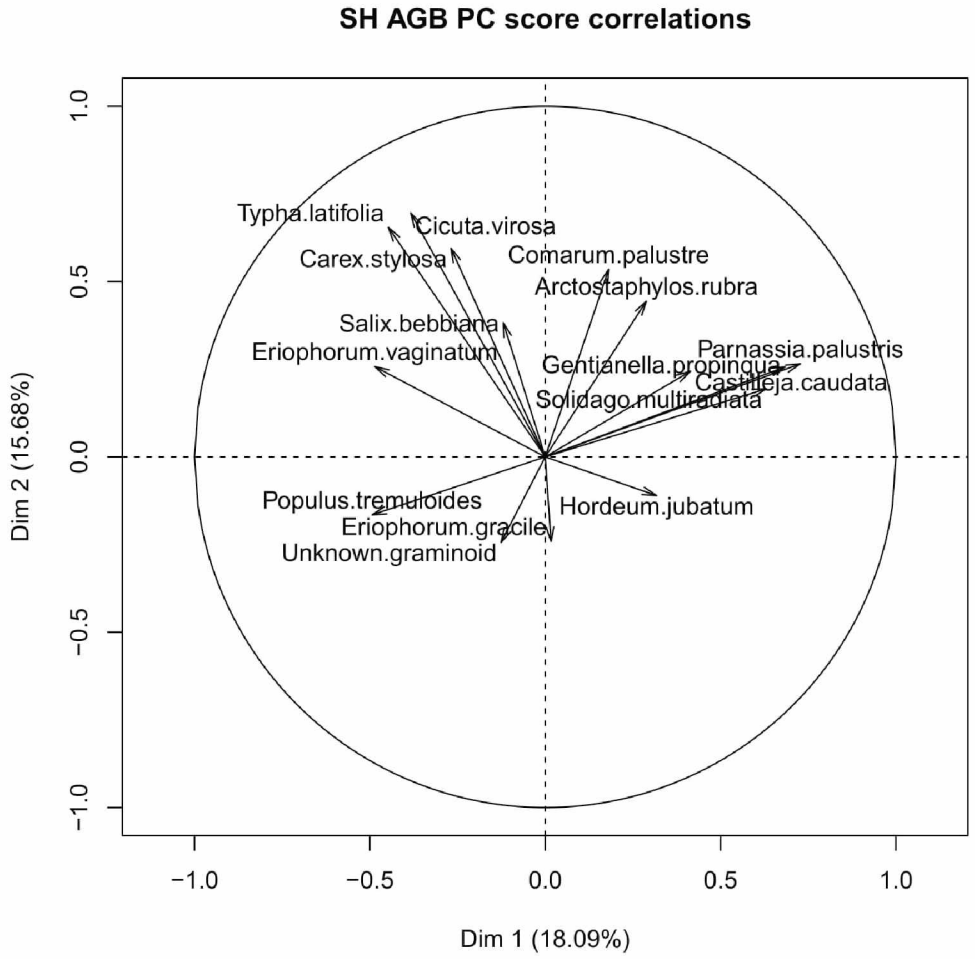

Figure A.2. Shrub (SH) community Principal Components Analysis. Arrows show with individual above-ground biomass (AGB) idiosyncratic species abundance. Axis 1 scores were used as an index of idiosyncratic species presence/absence.

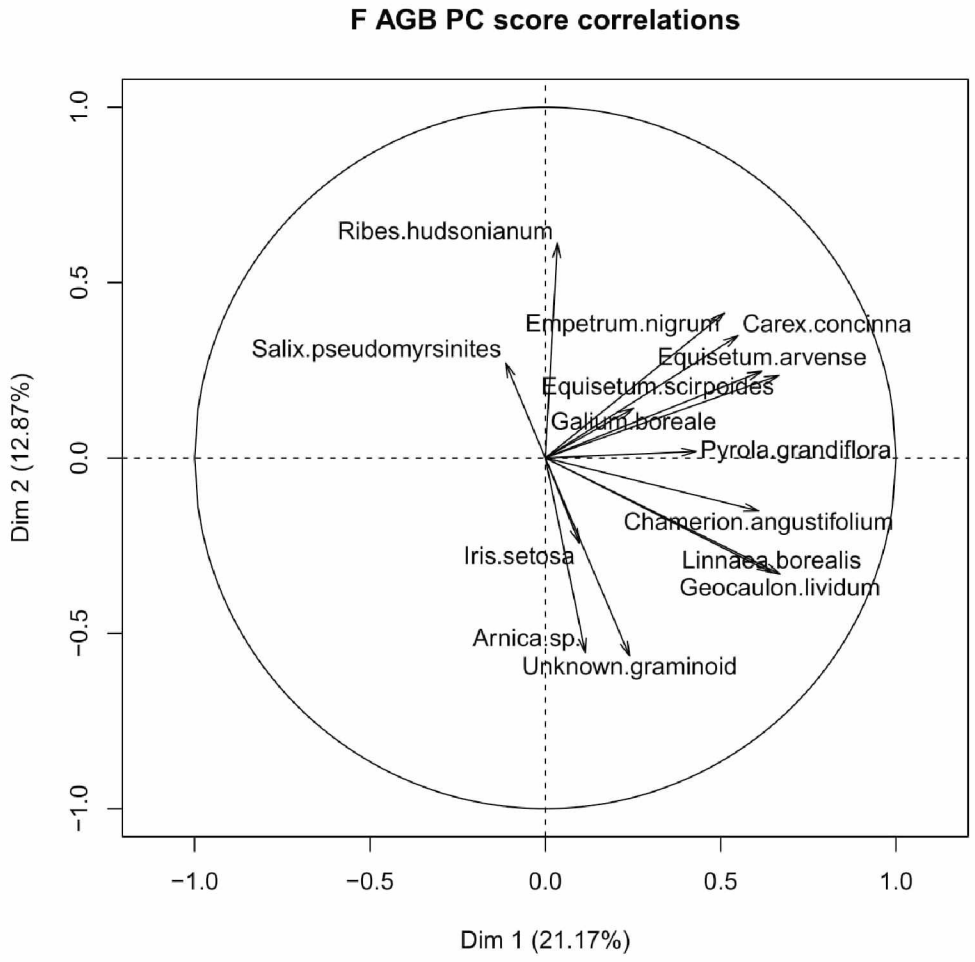

Figure A.3. Upland forest (F) community Principal Components Analysis. Arrows show correlations with individual above-ground biomass (AGB) idiosyncratic species abundance. Axis 1 scores were used as an index of idiosyncratic species presence/absence.

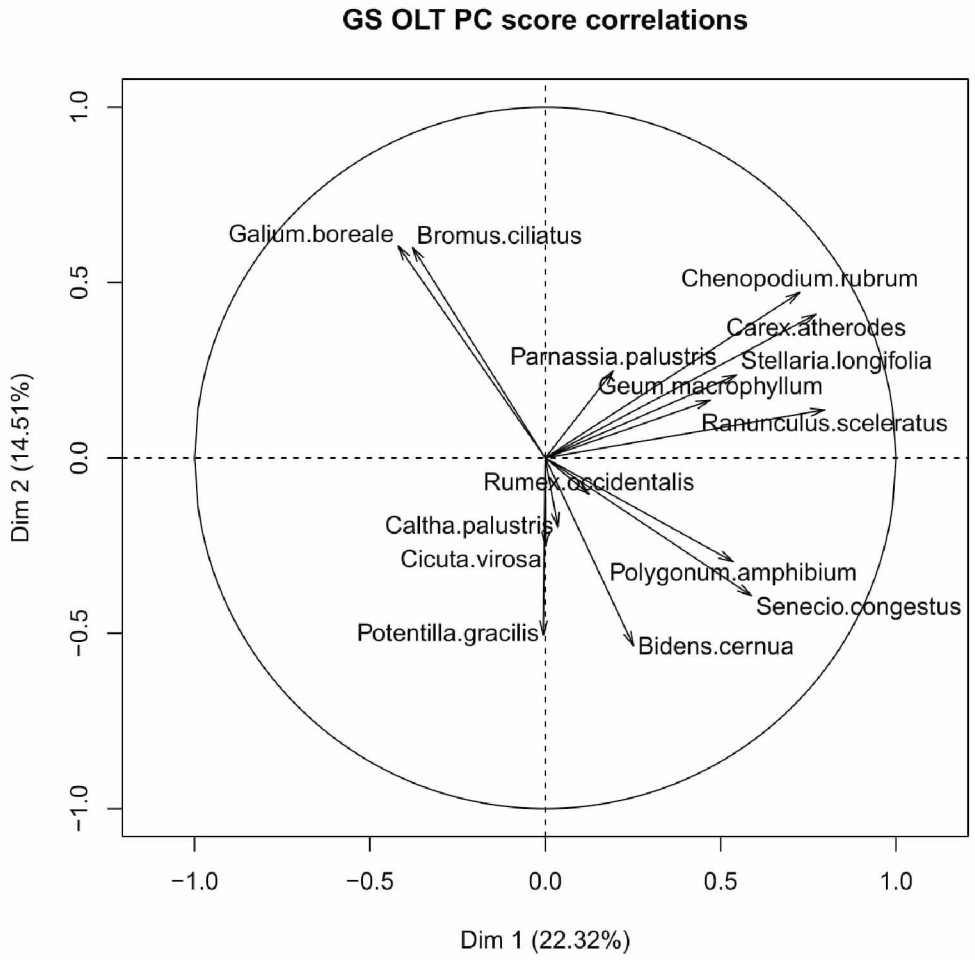

Figure A.4. Grass/Sedge (GS) community Principal Components Analysis. Arrows show correlations with individual organic layer thickness (OLT) idiosyncratic species abundance. Axis 1 scores were used as an index of idiosyncratic species presence/absence.

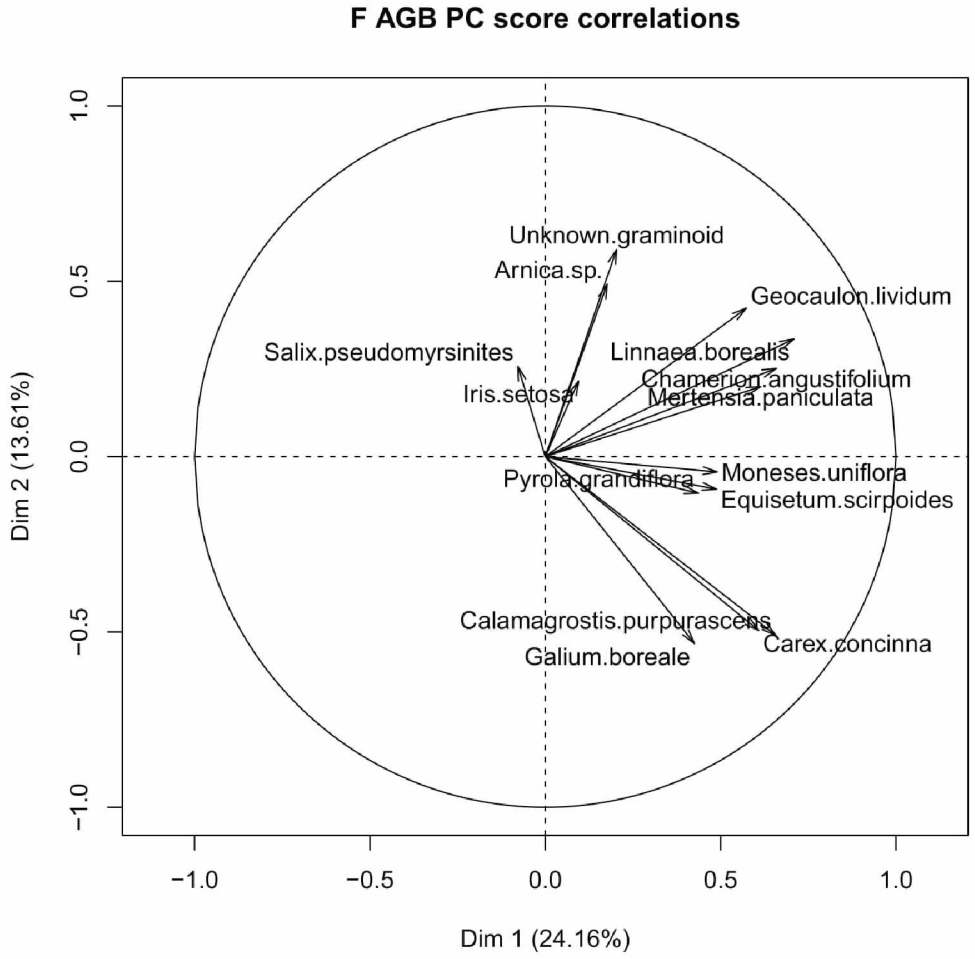

Figure A.5. Shrub (SH) community Principal Components Analysis. Arrows show correlations with individual organic layer thickness (OLT) idiosyncratic species abundance. Axis 1 scores were used as an index of idiosyncratic species presence/absence.

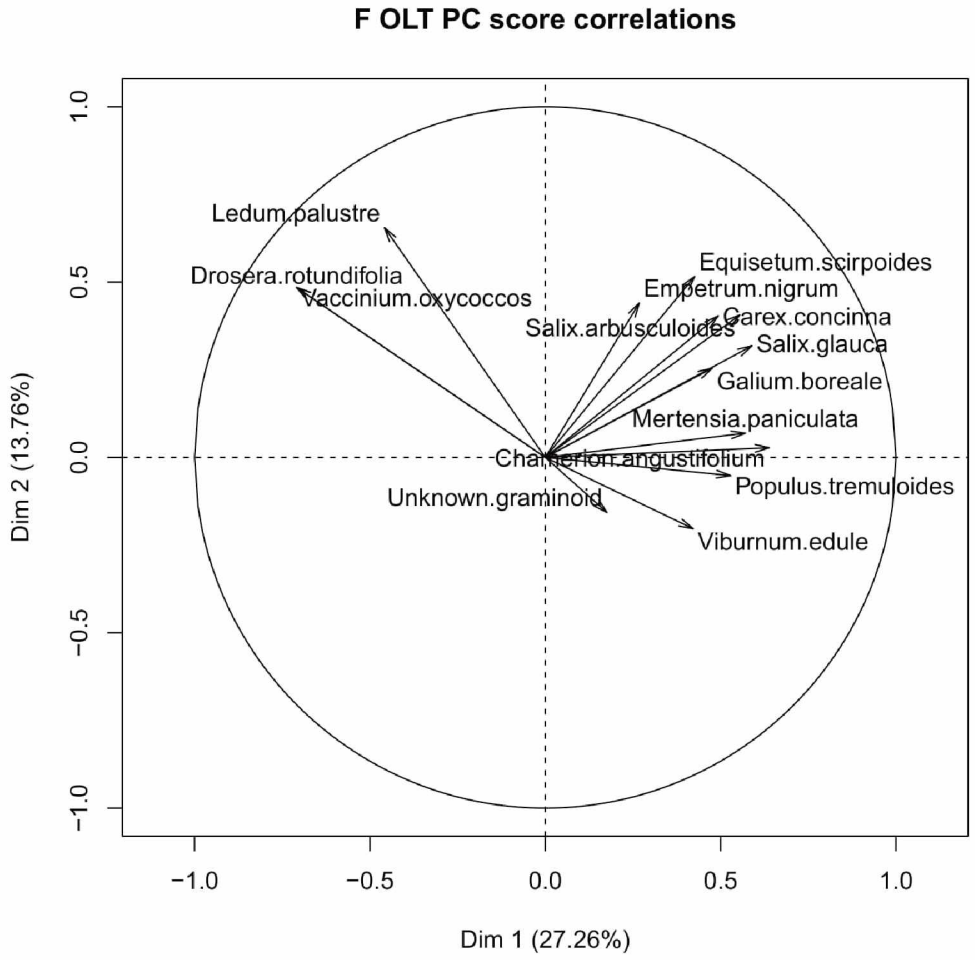

Figure A.6. Forest (F) community Principal Components Analysis. Arrows show correlations with individual organic layer thickness (OLT) idiosyncratic species abundance. Axis 1 scores were used as an index of idiosyncratic species presence/absence.

Chapter 3 : Landscape influences on water chemistry in boreal Alaskan lakes[1]

Abstract

Boreal lakes can play an important role in carbon budgets, because they simultaneously respire organic matter inputs and store organic carbon via sedimentation. Nutrient and carbon inputs also determine productivity and water quality of lakes, which can in turn affect their value as wildlife habitat and water sources for people. Long-term reductions in lake surface area have been observed throughout boreal Alaska in recent decades, but the consequences of these trends for nutrient and carbon dynamics in lakes are still unclear. I constructed alternative models to explain variation in carbon, nitrogen, and conductivity within boreal lakes using five categories of landscape charcteristics: terrestrial land cover, freshwater land cover, fire history, soil characteristics, and lake surface area dynamics (long-term shrinking trends and inter-annual variability). I then evaluated the relative influence of each component by fitting models in a random forest framework using a spatially balanced representative sample of 130 lakes from the Yukon Flats National Wildlife Refuge in northern Alaska. I found that N content, inorganic solutes, and dissolved organic carbon were highest at lakes surrounded by large herbaceous wetlands, which suggests that lake chemistry was sensitive to inputs derived from terrestrial sources. However, lake depth was also an important predictor of water chemistry. The shallowest lakes had nitrogen and organic carbon concentrations that were orders of magnitude higher than average, probably due to evapo-concentration. The relative influence of land cover and lake-specific characteristics such as depth varied between lakes whose surface area was shrinking, stable, or fluctuating, which is consistent with the hypothesis that lake surface area dynamics mediate hydrologic connectivity between lakes and the surrounding landscape. Overall, my results highlight the importance of terrestrial-aquatic interactions for understanding nutrient cycling and carbon source-sink dynamics in lowland boreal landscapes.

[1] Patil, V. P., D. B. Griffith, S. E. Euskirchen, A. D. McGuire, and M. P. Waldrop. Landscape influences on water chemistry in boreal Alaskan lakes. Prepared for Landscape Ecology.

Introduction

Climate warming at high latitudes has caused significant reductions in both the abundance and the size of lakes in subarctic ecosystems (Riordan et al. 2006; Smol and Douglas 2007; Roach et al. 2011). Lakes are an abundant feature in these landscapes due to the presence of discontinuous permafrost, which prevents drainage of surface waters (Roach et al. 2013). The mechanisms that link warming to lake shrinkage have been the subject of intense research, primarily in Alaska. These mechanisms include shallow and deep permafrost thaw, increased evaporation/inflow ratios, and terrestrialization (Yoshikawa and Hinzman 2003; Roach et al. 2011; Minsley et al. 2012). Less attention has been paid to the ecological consequences of these changes, which are still poorly understood.

One response to boreal lake shrinkage is an increase in nutrient and ion concentrations, which appears driven by solute evapo-concentration (Lewis et al. 2014a), as well as variation in groundwater connectivity (Roach et al. 2011; Minsley et al. 2012). The latter mechanism could help to explain why shrinking and non-shrinking lakes frequently occur adjacent to each other, while experiencing the same climate regime. Changes in nutrient cycling and chemical inputs can result in eutrophication, reduced water quality for human consumption, changes in the composition of lake food webs and adjacent wetland plant communities, and altered rates of carbon (C) flux (Gergel et al. 1999; Cole et al. 2007; Lewis et al. 2014a). However, lake water chemistry is also regulated by the landscape in which a lake resides, described by variables that include soil properties, disturbance, land cover, lake-specific characteristics such as size, shape, and bathymetry (Soranno et al. 2010), and hydrologic connectivity (Fig. 3.1). The effects of lake shrinkage could be relatively unimportant for explaining variation in water chemistry in landscapes if other landscape context components exert more influence, as described below:

Soil properties

Within Alaska, lateral permafrost thaw and deepening of the active layer have been identified as mechanistic drivers of lake shrinkage (Jepsen et al. 2012). However, increased lateral groundwater flow can also improve a lake's water balance, as long as that lake sits at the bottom of a hydraulic gradient. Where the net flow of groundwater into a lake is positive, surface thaw can also increase the input of terrestrially derived nutrients by allowing groundwater to leach through a larger volume of soil (Walvoord et al. 2012). Finally, the chemical composition and dissolved organic matter content of groundwater inputs to lakes are also affected by the peat content of surrounding soils (Gergel et al. 1999).

Wildfire

The primary disturbance agent in the boreal biome is wildfire, which predisposes boreal lakes towards shrinkage, presumably by removing soil insulation, creating shallow groundwater flow paths via permafrost degradation, and causing increased evaporation by reducing albedo in adjacent terrestrial environments (Roach et al. 2013). Fire can also influence C and nutrient inputs by removing organic matter from the surrounding landscape that could otherwise be exported to lakes, and by promoting the mobilization of nutrients from thawing organic soil while simultaneously reducing uptake by plants (Bayley et al. 1992; O'Donnell et al. 2011; Yuan et al. 2012).

Land cover

Land cover has been identified as a primary driver of lake water chemistry at multiple scales, ranging from the watershed to the lakeshore (Soranno et al. 2010). In particular, the proportion of wetland cover near lakes is positively correlated with dissolved organic matter in north temperate and boreal lakes (Gergel et al. 1999). This relationship appears to be robust across scales and at a wide range of latitudes (Gergel et al. 1999; Larsen et al. 2011), suggesting that it may be more influential than other types of landscape context. Terrestrial vegetation is also an important source of nitrogen (N) in lakes, including both organic and inorganic forms (Neff et al. 2003).

In the context of lake water chemistry, land cover also includes the proximity and size distribution of surface water features, including both adjacent lakes and streams. In lowland boreal environments, lakes undergo seasonal expansion after spring snowmelt, and may merge and exchange water with other surface features during this period. As a result, even isolated lakes with no permanent surface inflow or outflow channels can be temporarily connected to other lakes and streams if they are close enough, although this connectivity is also a function of inter- and intra-annual variation in lake size, as discussed in the next section.

Lake area change/Hydrologic connectivity

Hydrologic connectivity between lakes and the surrounding landscape is widely recognized as a control over water chemistry (Martin and Soranno 2006). Connectivity is typically described in terms of the presence of inflow streams and upstream lakes. However, many boreal and subarctic lakes are closed-basin lakes created by thermokarst (Yoshikawa and Hinzman 2003; Riordan et al. 2006). In these systems, standard connectivity classifications are of little use, and surface hydrologic connectivity is mainly a result of flooding. Both stable and shrinking boreal lakes can undergo dramatic seasonal and year-to-year changes in surface area driven by the timing and volume of snowmelt and summer

precipitation. The magnitude of these fluctuations frequently dwarfs the annual rates of change of shrinking lakes (Roach et al. 2011). As a result, while a third of boreal Alaskan lakes may be smaller than they were 30 years ago, less than 10% exhibit statistically significant rates of change (Rover et al. 2012). Water-level fluctuations (flooding) could affect water chemistry because they provide a mechanism for importing dissolved and particulate organic matter from terrestrial sources and other water bodies, and because wet/dry cycles make organic matter more susceptible to decomposition and leaching (Lundquist et al. 1999; Stepanauskas et al. 2000; Asada et al. 2005). At the same time, lake shrinkage could be both a symptom and a positive feedback mechanism for reduced subsurface hydrologic connectivity between lakes and other landscape context components, because shrinkage rates appear to be driven by the balance between groundwater recharge and evaporation. In this sense, flooding, shrinking and stable lakes may represent distinct connectivity classes, with flooding and shrinking lakes experiencing higher and lower connectivity, respectively, when compared to stable lakes (Fig. 3.1).

Lake-specific characteristics

The effect of shrinking trends on water chemistry may be strongly related to intrinsic characteristics of lakes, such as average and maximum depth, area, shoreline length, shape, and other physical properties of a lake basin (Carpenter 1983). These properties affect residence time, which is the time it takes for a unit of water to move through a lake, and also determine the surface area of the lake-bottom:sediment interface where chemical exchanges between lakes and the surrounding landscape can occur (Carpenter 1983; Fergus et al. 2011). Maximum depth is a strong predictor of lake nutrients and ion concentrations regardless of lake size, ecoregion, or landscape context (Read et al. 2015). Although shrinking due to evaporation is likely to increase the concentration of ions in any lake, these effects may only be detectable in lakes with shallow bathymetric profiles and short residence

time, where nutrients in the water column do not have time to be removed through biological processing, flocculation, and other processes. Although lake depth and lake size are intuitively related, lake bathymetric profiles can be so variable that there may be no relationship between lake shrinkage and maximum depth (Wantzen et al. 2008).

The five landscape context components described above (lake area change/hydrologic connectivity, soils, wildfire, land cover including vegetation and surface water, and lake-specific characteristics) are all potentially significant drivers of water chemistry. I examined the separate and combined influence of these drivers on a suite of five water chemistry variables that are strong indicators of chemical exchange between terrestrial and aquatic systems, and which are also relevant for understanding the effects of changing water chemistry on biodiversity, productivity, and C storage. These water chemistry variables were dissolved organic carbon (DOC), total dissolved nitrogen (TDN), dissolved inorganic nitrogen (DIN; estimated as $NO_3 + NH_4$), dissolved organic nitrogen (DON; estimated as TDN – DIN), and electrical conductivity (conductivity).

DOC plays an important role in regional C cycling (Laudon et al. 2011). Boreal peatlands have historically been a net C sink due to the combination of low temperatures and anoxic, saturated soils that allow organic matter to accumulate faster than it can decompose (Benoy et al. 2007). However, a significant fraction of terrestrially derived organic C in boreal peatlands is exported to lakes, where it frequently accounts for the majority of DOC (Cole et al. 2007; Olefeldt et al. 2013). This allocthonous (externally sourced) DOC provides energy for microbial respiration, and DOC concentrations have been linked to CO_2 efflux in boreal lakes around the world (Larsen et al. 2011). At the same time, humic and fulvic DOC inputs from peatlands can reduce primary production and CO_2 uptake in lakes by reducing light penetration (Gergel et al. 1999). Lake shrinkage could reduce groundwater flow and DOC export from wetlands to lakes. Quantifying that relationship could help clarify whether lake area dynamics represent a positive or negative feedback to atmospheric C concentrations.

Terrestrial-aquatic exchange of organic matter can regulate the cycling of N and other nutrients, in addition to C (Neff et al. 2003). Traditionally, lake ecosystems have been viewed as phosphorous limited, but more recent studies have emphasized the potential importance of N as a limiting or co-limiting nutrient that can regulate primary production and cause eutrophication (Grimm et al. 2003). N can be exported to lakes from the landscape in both organic and inorganic forms, which move via different pathways and have unique implications for water quality and lake metabolism/productivity (Neff et al. 2003).

Inorganic N, which exists in boreal lakes primarily as NO_3 and NH_4, is readily accessible to phytoplankton, and is therefore directly related to primary production (Bronk et al. 2007). NO_3 is the most likely inorganic form to be exported from terrestrial systems, since it does not adsorb to soils as readily as NH_4 cations, but the amount actually exported to lakes is typically low due to rapid biological uptake during subsurface flow through the surrounding soil environment (Grimm et al. 2003). The exceptions to this rule are N-saturated soils, which are most commonly caused by human N subsidies and atmospheric deposition (Grimm et al. 2003). However, inorganic N export could also be promoted by lake shrinkage, because the drying of formerly saturated soils near shrinking lakes could promote increased N mineralization. At the same time, lake shrinkage through evaporation could concentrate dissolved NO_3 in lakes, as has been observed for total N (Chapin et al. 2011; Lewis et al. 2014a). NO_3 concentrations in boreal lakes could also be increased by flooding, since wet/dry cycles in wetlands soils promote microbial activity and mineralization while also providing a mechanism for newly mineralized N to be immediately flushed into adjacent lakes (Jenerette and Chatterjee 2012). In addition, permafrost thaw allows groundwater to flow through N-rich, previously frozen mineral soil layers, and has been linked to DIN export in boreal streams (Walvoord and Striegl 2007). Lake area change and soil or permafrost properties are therefore likely to be useful predictors of nutrient status and productivity in boreal lakes as well.

Nitrogen can also be exported to lakes in organic forms, which include amino acids as well as more complex compounds such as proteins and condensed phenolics (Stepanauskas et al. 2000). In boreal streams underlain by permafrost, DON makes up a large fraction of total N inputs because precipitation and groundwater are constrained to flow through shallow organic layers rather than deep mineral soil (Walvoord and Striegl 2007). Until recently, all DON was considered unavailable to aquatic primary producers, but recent work suggests that amino acids and other organic N compounds can be accessed by phytoplankton almost as readily as inorganic N (Bronk et al. 2007). However, labile organic N compounds, specifically amino acids, are tightly cycled between soils and vegetation in boreal ecosystems (Neff et al. 2003). As a result, most of the terrestrial DON that is available for export, and most of what occurs in boreal streams, consists of recalcitrant forms other than amino acids and urea (Stepanauskas et al. 2000). These recalcitrant DON compounds must be broken down by microbial respiration before they become available to primary producers. If the same holds true for boreal lakes, phytoplankton probably cannot directly take up most of the terrestrially derived DON being exported into those lakes, and the ratio of organic vs. inorganic N inputs could have significant implications for lake metabolic balance.

I included conductivity as a response variable because it can be used as an indicator for the concentration of conservative ions (Hauer and Lamberti 2011). In-lake C and N concentrations are influenced by microbial uptake as well as physical processes like flocculation and photodegradation, but conductivity is insensitive to biological activity (Waiser et al. 2006; Lewis at al. 2014). As a result, comparing the responses of C, N, and conductivity to lake-specific variables can clarify the extent to which variation in C and N is associated with biological or physical processes (Waiser 2006; Lewis et al. 2014a). I hypothesized that conductivity would be related to driving variables that regulate inputs and outputs of water and ions, including land cover (vegetation and surface water), lake shrinkage, and

flooding, but would not be strongly associated with lake-specific properties, which relate to residence time and opportunities for biological processing (Waiser 2006).

My goal in this study was to evaluate the relative importance of lake shrinkage as a driver of water chemistry compared to other components of a lake's landscape context. I asked the following questions: 1) Which group of variables (soils, wildfire, terrestrial land cover within 100m, freshwater land cover within 5km, lake-specific characteristics, or lake area change/hydrologic connectivity) were strong predictors of DOC, DON, DIN, TDN, and conductivity? 2) Were different water chemistry measurements responsive to different sets of landscape characteristics, and what did these contrasts mean for biogeochemical cycling in shrinking and non-shrinking lakes? 3) Did lake area dynamics (shrinking and flooding) affect hydrologic connectivity and mediate the influence of other landscape characteristics on water chemistry? I addressed these questions using data from a spatially balanced random sample of lakes in the Yukon Flats National Wildlife Refuge (YFNWR) of Alaska (Fig. 3.1), a boreal floodplain environment where widespread lake shrinkage has been well documented (Roach et al. 2011).

For my first question, each landscape context component represented a plausible alternative hypothesis for explaining variation in water chemistry, and each of these hypotheses led to testable predictions. First, I hypothesized that the relative importance of lake-specific characteristics would depend on the extent to which a water chemistry variable was controlled by in-lake biological and chemical processing. I based this hypothesis on the rationale that lake-specific characteristics, particularly depth and bathymetry, are related to residence time and processing time (Read et al. 2015). I therefore predicted that, out of all five response variables, inorganic N, which is readily taken up by lake primary producers (Khalili et al. 2010) would be most strongly associated with lake-specific characteristic variables such as maximum depth, and predicted that conductivity would show the weakest association with lake-specific variables. Between DOC and DON, I expected DOC to show

stronger association with lake-specific variables, because it is more susceptible to UV degradation in addition to being available for uptake by microbes (Olefeldt et al. 2013). In summary, I expected the following pattern in predictive power for lake-specific component models: DIN > DOC > DON > conductivity. I also predicted that lake area dynamics (flooding and shrinking), would be most strongly associated with DIN, because flooding, soil drying, and evaporation are likely to control mineralization, leaching, and in-lake concentration (Chapin et al. 2011; Jenerette and Chatterjee 2012; Lewis et al. 2014a). In contrast, DOC and DON could be transported from land to lakes through groundwater even in stable hydrologic conditions where lake-margin soils remain saturated and anoxic. Finally, I predicted that terrestrial land cover variables (e.g. graminoid zone width) would be most strongly correlated with organic variables (DOC and DON) due to the influence of land cover on the chemical properties of groundwater and adjacent water bodies (Gergel et al. 1999). Conversely, inorganic lake inputs (DIN and conductivity), which derive more from groundwater flow through mineral soil, were predicted to be correlated more strongly with soil variables than with land cover (Walvoord and Striegl 2007).

For my second question, I hypothesized that relationships between water chemistry and major driver variables would be affected by lake area dynamics. Specifically, I expected fluctuating lakes to show the strongest correlations between water chemistry and freshwater land cover. In contrast, I predicted that shrinking lakes would show weak or non-significant correlations with freshwater land cover variables when compared to stable and fluctuating lakes, but would show the strongest correlations between water chemistry and lake-specific variables.

I also interpolated the distribution of C, N, and conductivity values across the entire YFNWR, which includes both federal and private/Native corporation land (Fig. 3.2), to address the management implications of this study. I estimated the mean summer concentration and variability of each water chemistry variable as a function of land ownership. Yukon Flats lakes provide habitat for fish and

wildlife resources used by both recreational visitors and local subsistence hunters, and also provide fresh water for residents. As such, water chemistry is a potentially useful factor for refuge managers to consider when developing land exchange programs or other management actions.

Methods

Analytical framework

I tested alternative hypotheses using a multi-model framework. I constructed multivariate random forest regression tree models (Cutler et al. 2007) containing sets of predictor variables that represented each class of hypothetical water chemistry drivers (Table 3.1; Fig. 3.1). I also created a combined model that included predictors from all models, making it possible to rank individual variables by predictive power and identify important interactions among predictors (Table 3.1). I repeated this analysis for each of the five water chemistry measurements.

Study Area

I examined sources of variation in water chemistry at 130 lakes distributed within the YFNWR in northeastern Alaska (66.33° N, 146.00° W; Fig. 3.1). This area is uniquely appropriate for studying the influence of lake size dynamics on water chemistry and terrestrial-aquatic interactions. The YFNWR encompasses 3.5 million hectares surrounding the Yukon River floodplain, and consists of a complex mosaic of lakes, wetlands, and upland forest (Gallant 1995). YFNWR contains approximately 40,000 lakes. The abundant surface water in the region is maintained by discontinuously distributed permafrost, which prevents drainage and promotes ponding (Roach et al. 2011). Lake shrinking trends within the refuge span the full range of variation observed across the state, and many lakes exhibit large inter-annual fluctuations in size that obscure long-term trends (Rover et al. 2012; Roach et al. 2013). Terrestrial land cover is also variable, with some lakes surrounded by upland forest, while others are

separated from the forest by rings of graminoid fen or deciduous shrub-dominated communities (Chapter 2).

Study Design

During June – August of 2010 and 2011, I surveyed 48 focal lakes as well as 75 satellite lakes adjacent to focal sites, for a total of 130 lakes. I selected candidate focal sites from a GIS layer of floatplane-landable lakes (since the study area is inaccessible by road) using Agile Statistics software to generate a Generalized Random Tessellation Stratified (GRTS) sample (Stevens and Olsen 2004). This method ensured that sample sites comprised a spatially balanced, random sample of the study area (Stevens and Olsen 2004). Sampling efforts were divided between two strata on either side of the Yukon River that had opposite regional lake area trends since 1985. The North stratum has been characterized by increasing and stable lake size trends, while the south side has been estimated to have an overall decreasing trend (Roach et al. 2013). Candidate lakes that could not be accessed by floatplane (e.g. lakes that became too shallow to land on due to seasonal drying) were replaced with the nearest landable lake. All lakes within a 1- km radius of the focal lake centroid that could be accessed within 14 days of landing were sampled as satellite lakes. This design allowed me to include small, unlandable lakes in the sample population, and to account for the potential effects of spatial autocorrelation between nearby lakes.

Lake trend classification

I estimated trends in lake area between 1979 and the present using a time series of 22 Landsat satellite images. These images were converted to GIS lake maps as part of a larger study on long-term lake trends in the YFNWR (Rover et al. 2012). I used a minimum of six images per lake to ensure adequate trend estimation. Because adequate Landsat coverage was not available for all lakes, this

reduced the sample size to 111. After extracting area measurements for each lake in each year where imagery could be obtained, I fit linear regression models of lake surface area as a function of year and day of year (Roach et al. 2011; Equation 3.1).

(3.1) $$Lake\ Area = \beta_1 * Year + \beta_2 * Day\ of\ year$$

Lakes with significant model F statistics and significant negative Year coefficients were characterized as shrinking. I assessed statistical significance using an alpha cutoff of 0.05. The lake sample included 18 significantly decreasing lakes, representing 17% of the total sample population. I also found that three lakes had significant increasing trends. I chose to exclude these three lakes from analysis due to the small sample size, and because increasing lakes represent a small fraction of the total landscape (<3%) in YFNWR and elsewhere in Alaska (Rover et al. 2012; Roach et al. 2011). This yielded a final sample of 108 lakes.

I characterized flood dynamics based on the presence of variability in lake size that could not be accounted for by linear annual or seasonal trends. This involved calculating an index of the root mean squared error coefficient of variation (CV(RMSE)) for the linear trend models I fit for each lake. I developed the CV(RMSE) to reflect the amount of dispersion in the response variable (lake area) that is not accounted for by the linear model, and is standardized to the mean size of each lake. The standard coefficient of variation (CV), which is calculated as the standard deviation/mean value of size measurements, has previously been used to characterize inter-annual variability in shrinking lakes (Roach et al. 2011), but CV(RMSE) should more accurately characterize inter-annual water-level fluctuations because large CV values could result from a strong but consistent decreasing trend as well as inter-annual variability. I classified lakes as flooding or not based on whether their CV(RMSE) values exceeded the 75th percentile, which represented a clear breakpoint in the data. No lakes classified as flooding showed significant increasing or decreasing trends. I identified 24 flooding lakes.

To verify that these results were representative of the region, I also calculated CV(RMSE) values for several thousand lakes in the central Yukon Flats using a dataset generated by Rover et al. (2012).

Predictor Variables: Soil

I expected soil properties related to thaw depth, porosity, and organic matter content to influence the flow of dissolved nutrients and ions into lakes from the surrounding landscape. I therefore included field measurements of peat depth at the lakeshore and at the boundary between lake-margin wetlands and upland forest. I also included remotely sensed estimates of mean active layer thickness and probability of permafrost occurrence within 100m of the water's edge (Pastick et al. 2013) in the soil effects model (Table 3.1).

Predictor Variables: Terrestrial land cover

Because the entire Yukon Flats ecoregion has extremely low topographical relief, estimating watershed size for a given lake is impractical. Instead, I characterized landscape influences within a 100m buffer around lakes. I classified land cover within this buffer using a combination of field measurements and remote sensing data. Vegetation surveys were conducted at each lake on four 100m transects running perpendicular to the water's edge. I identified the position of boundaries between community types along each of these transects based on the tallest plant growth forms (graminoid/non-woody forbs vs. multi-stem deciduous shrubs vs. trees) with >50% cover. I then estimated community type area within 100m of the lakeshore by creating plant community buffers around lake perimeters in ArcGIS based on the locations of these transitions. The final dataset included size estimates for the graminoid wetland zone, as well as for emergent littoral and floating mat plant communities. I also characterized community type diversity in the 100m buffer using modified Shannon indices with community size as a surrogate for abundance (Equation 3.2),

(3.2) $$H = -\sum_{i=1}^{S} p_i \times \ln p_i$$

where H = Shannon diversity, p_i = the proportional abundance of community i along a transect, and S = the total number of communities present. Finally, I estimated the total above-ground plant biomass and the mean biomass per hectare within the 100m buffer using a field-validated, remotely-sensed above-ground biomass map for the region (Ji et al. 2012).

Predictor Variables: Freshwater Land cover

Freshwater landscape variables included the distance to the nearest river, the nearest stream of any size, the mean, maximum, and standard deviation of lake size and the total number of lakes within a 5-km radius of each site. All surface water variables were derived from the National Hydrography dataset (nhd.usgs.gov). These variables were meant to reflect the potential for groundwater exchange between study lakes and other water bodies, and for surface connectivity during flood events.

Predictor Variables: Lake-Specific Variables

There is increasing evidence that lake-specific characteristics, especially basin morphology, are a primary influence on water chemistry across a broad range of landscape contexts and disturbance regimes (Read et al. 2015). I represented lake-specific effects using GIS estimates of lake shoreline length, area, and the ratio of lake shoreline to the perimeter of a circle with the same surface area. This last variable was meant to capture the roundness or tortuosity of each lake's shoreline (Kalff 2002). I also calculated maximum lake depth from field bathymetry measurements taken at 10m intervals along 4 perpendicular transects meeting at the centroid of each lake. Maximum depth is a strong predictor of nutrient and ion concentrations in lakes throughout the United States, and is correlated with residence time (Read et al. 2015). Finally, I estimated surface/volume ratios by estimating lake volume assuming that depth increased linearly from the shore to the deepest point. This estimate was proportional to the inverse of lake depth.

Water chemistry data

I measured conductivity using a handheld probe (YSI Professional Plus) *in-situ*, 0.5 m below the water surface near the center of each lake. For other water chemistry measurements, I collected 1-liter water samples at 0.5 m depth, which were kept cool until they could be flown out within a few days. TDN, DOC, nitrate, and ammonium measurements were made following standard U.S. Geological Survey protocols (Wilde et al. 1998). To confirm that conductivity reflected the abundance of conservative ions rather than nutrients such as nitrate and ammonium, I tested for significant linear relationships between conductivity, nitrate, ammonium, and four major (i.e. common) conservative ions: Na, Ca, Mg, and SO_4 (Halm and Griffith 2014). Water chemistry data are publicly available through the U.S. Geological Survey (Halm and Griffith 2014).

Analysis

I evaluated the relative support for all hypotheses by fitting candidate models using the random forest algorithm, each of which contained 3-6 variables that collectively represented an aspect of landscape context, as well as a combined model that included all predictor variables (Read et al. 2015). Each model also included the Julian day as a predictor, to control for seasonal effects on water chemistry measurements. Random forest analysis involves the generation of hundreds of regression tree models for a given response variable, each of which uses a randomly selected subset of the available data and a random subset of the predictor variables contained in the model being tested (Cutler et al. 2007). Each tree model is evaluated by testing its predictive ability using the data withheld during its generation (Cutler et al. 2007). The predictive power of the overall random forest model is estimated by averaging the percent variance explained by each individual regression tree (Cutler et al. 2007). Random forest models implicitly account for interactions among predictor

variables, and are robust in the face of multicollinearity and non-linearity (Liaw and Wiener 2002; Archer and Kimes 2008). These characteristics make them a superior alternative to more common analytical techniques, such as generalized linear modeling, that are used to examine complex multivariate hypotheses. Random forest models have been used previously to estimate the influence of land cover variables at multiple scales on water chemistry, algal blooms, and other water quality parameters (Kehoe et al. 2012; Read et al. 2015; Hollister et al. 2016).

I used model-averaged percent variance explained to assess the relative support for each alternative hypothesis (Archer and Kimes 2008). This metric, which is a function of the mean squared error divided by the variance of the response, provides a 'pseudo R-squared' that can be interpreted similarly to a standard R^2 except that it can also produce negative values indicating very poor model fit (Archer and Kimes 2008). I also estimated variable importance scores for each predictor variable in the combined model. Variable importance was estimated by permuting the values of a variable with replacement, re-fitting the random forest model and computing the mean change in model mean squared error, then repeating this process 500 times and averaging the results (Archer and Kimes 2008). The average change in model mean squared error reflected the effect of each predictor on model performance while accounting for the influence of all other variables and interactions among them. Standardized importance values were calculated by dividing raw importance scores by the maximum variable importance in each model. These standardized values were comparable across models and across response variables (Read et al. 2015), and they complemented the multi-model comparison by highlighting variables that best represented each class of hypothetical water chemistry drivers. Finally, to verify that the predictive strength of the combined model was not simply a function of the number of included predictor variables, combined models were re-fit using only the top five predictors, and these reduced models were compared to the original model (Read et al. 2015).

Variable importance scores alone are not an ideal tool for testing alternative hypotheses, because they cannot be used to assess the strength or sign of an association between two variables. I therefore also estimated effect size using partial dependence plots, which showed the average shape, direction, and strength of the relationship between predictor variables and water chemistry measurements (Archer and Kimes 2008). Effect size was estimated by dividing the y-axis range of a plot, which represented the range of variation in the response variable that could be accounted for by a predictor variable, by the total observed range of the response variable. These values indicated the proportion of variation in the response that could be attributed to a predictor variable. I also tested for linear correlations between predictor variables and water chemistry variables separately for flooding, shrinking, and stable lakes.

Results

Overall, top models explained ~40-55% of variance in water chemistry variables, except for DIN (Table 3.2). No model for DIN had a detectable level of predictive power (> 0 % variance explained) except for the soil model and the model with the top five variables combined, which only explained 1% and 3% of observed variation in DIN, respectively (Table 3.2). The remaining four water chemistry variables (DOC, DON, TDN, and conductivity) showed strikingly similar patterns of relative model fit, with lake change, land cover, and soil models all explaining between 25 and 43% of observed variance in response variables (Table 3.2). Lake change models slightly outperformed other models of conductivity, DOC and TDN, while freshwater land cover models were the top predictor of DON. Fire history models had essentially zero predictive power for all water chemistry variables (percent variance explained <0; Table 3.2). DON showed a slightly different pattern than DOC, TDN, or conductivity, in that the lake-specific variables model was a substantially better predictor of DON than the lake- change model (42% variance explained versus 35%; Table 3.2). However, DON tracked TDN closely in terms of the relative influence of different landscape context components (Table 3.2).

Although combined models had four to five times the number of predictor variables used for any component model, including all the variables listed in Table 3.1, this additional complexity cannot solely account for the combined models' increased predictive power. Most of the combined model predictive power could be accounted for by the five variables with the highest importance rankings for each response (Table 3.2). Combined models did a slightly better job of predicting N variables than DOC, but explained between 49 and 57% of observed variance in DOC, DON, and TDN (Table 3.2). In contrast, the combined model of conductivity only explained 37% of observed variance.

In the combined (all variables) models, predictor variable importance rankings were similar for all response variables except for DIN (Fig. 3.3). Due to the poor performance of DIN land cover, lake change, lake-specific, wildfire, and soil models, I did not have confidence in the variable importance rankings from the DIN combined model and did not attempt to interpret the biological significance of these rankings. Max depth and lake surface/volume ratio (lake-specific variables) consistently emerged as two of the predictor variables most responsible for model performance (Fig. 3.3). Both variables accounted for approximately 15% of the observed range in water chemistry values after adjusting for the influence of other variables (Fig. 3.3). Several terrestrial land cover variables were also top-ranked in combined models, including graminoid zone width, the Shannon index (a community diversity index) and floating mat zone width (Fig. 3.3). Of the three, graminoid zone width had the largest effect size, accounting for between 10 and 15% of observed variation in DON, DOC, TDN, and conductivity (Fig. 3.4). In contrast, floating mat width and the Shannon index only accounted for about 5% of observed variation in water chemistry measurements (Fig. 3.4). Field and remotely sensed active layer thickness, all soil variables, appeared in the top five rankings for at least one water chemistry measurement, but were generally outperformed by land cover and lake-specific variables (Fig. 3.3). However, forest edge active layer thickness had the fourth highest variable importance score in

conductivity models, and accounted for nearly 5% of observed variation in conductivity (Fig. 3.3; Fig. 3.4).

Despite the high predictive performance of lake change models for all response variables (Table 3.2), individual lake change variables did not receive high importance rankings. The notable exception was the Laketrend variable, which represented the average annual rate of change in lake size, and was the fifth most important predictor of conductivity in a combined model. However, many other conductivity predictors had higher effect sizes (Fig. 3.3). Freshwater land cover variables, which described surface water distribution, were also typically poor individual predictors of water chemistry, although the number and maximum size of lakes within a 5km radius both appeared in the final list of high-importance variables (Fig. 3.3). In particular, the number of other lakes nearby was linked with conductivity (Fig. 3.3). However, land-cover variables due to surface water distribution explained almost none of the observed variability in DON and DOC (Fig. 3.4).

The strength, functional shape, and direction of responses to top driving variables were consistent between DOC, TDN, DON, and conductivity (Fig. 3.5). The response to maximum depth, the top-performing, lake-specific variable, was highly non-linear, with the shallowest lakes containing dissolved organic C and N concentrations several orders of magnitude higher than the regional average (Fig. 3.5). Land cover and soil properties had similar nonlinear effects, in that lakes with the largest adjacent graminoid zones and deepest seasonal thaw or active layer thickness had substantially higher nutrient and ion concentrations than other sites (Fig. 3.5). Ion and nutrient concentrations tended to increase asymptotically with the size of nearby lakes, but this relationship could not account for the highest nutrient and ion concentrations I observed (Fig. 3.5).

Although the rate of lake area change (Laketrend) was a highly ranked predictor variable for water chemistry variables, particularly conductivity, in all lakes (Fig. 3.3), its effect size score was low

compared to most other variables with high importance scores. In addition, the influence of the Laketrend variable was strongly associated with the small number of lakes with increasing (positive) slopes (Appendix A - partial dependence plots). Because only three lakes in the sample had significant increasing trends, increasing lakes could not be statistically compared with stable and shrinking sites. Shrinking and flooding lakes did not differ significantly from stable lakes in terms of their chemical signatures when all lakes were analyzed together. However, when the four outlier lakes (C and N concentrations several orders of magnitude above average) were excluded, lake type classification was a significant predictor of both TDN and conductivity, and had a non-significant effect on DOC (Fig. 3.6). Those four lakes were all located within 1 km of each other, and all four lakes were classified as stable. For all response variables, shrinking lakes had higher median values relative to stable and flooding lakes (Fig. 3.6).

The distribution of shrinking, stable, and flooding lakes in the sample population was a reasonable representation of the Yukon Flats landscape, although the proportion of shrinking lakes was over-represented in the sample population compared to the distribution of shrinking lakes across the central Yukon Flats (Table 3.3). When analyzed separately, sample sizes for each lake type were deemed insufficient for a full random forest analysis (n= 18 shrinking, 19 flooding, 71 stable). Instead, I compared correlation coefficients between each response variable and the four top-ranked land cover driver variables across lake classifications. All response variables were negatively correlated with maximum lake depth and positively correlated with the land cover variable of graminoid zone width, but differed in terms of the strength and statistical significance of this relationship (Table 3.4). N and C concentrations were more strongly correlated with maximum depth in shrinking lakes than in the other two lake types, and the relationship between graminoid zone width and water chemistry was notably stronger at stable lakes compared to shrinking and flooding sites (Table 3.4). In flooding lakes, DOC,

TDN, and DON were all strongly positively correlated with maximum lake size (5km radius), a pattern that was not apparent for any response variable at stable or shrinking lakes (Table 3.4).

Inverse distance weighting-derived maps of water chemistry values had moderately high accuracy based on 10-fold cross-validation (R^2 for regression models of predicted values ~ observed values) = 0.55 for DOC, 0.53 for TDN, 0.44 for DON, and 0.38 for conductivity). Sensitivity analysis using cross-validation with 1000 replicates per parameter set indicated that an inverse distance weighting power of 2 and 5 nearest neighbors were the optimal parameter values, although mean cross-validated accuracy varied by less than 10% across all parameter combinations examined.

In addition to being driven by a similar set of landscape variables, DOC, TDN, DON, and conductivity showed similar spatial distributions across the study area (Fig. 3.7). The highest C, nutrient, and ion concentrations were located in the northwestern Yukon Flats, to the north of the Yukon River. Overall, lakes tended to be less eutrophic on the south side of the river, although several notable hotspots were apparent (Fig. 3.7). Federal lands within the Yukon Flats NWR had higher concentrations of all response variables, on average, than adjacent areas owned by local Native corporations and other private holdings (Fig. 3.8). All differences were highly significant based on one-way ANOVA (DOC: $F=391.52$, $df=1,4308$, $p < 0.0001$; TDN: $F=399.75$, $df=1,4308$, $p <0.0001$; DON: $F=344.43$,$df=1,4308$,$p <0.0001$; conductivity: $F=706.87$, $df=1,4308$, $p <0.0001$).

Discussion

Overview

In this study, I evaluated relationships between water chemistry and landscape characteristics in lowland boreal Alaskan lakes. My objectives were to assess the relative importance of lake shrinkage as a driver of water chemistry at the landscape scale, and to examine the role of lake area trends (shrinking and flooding) as mediators of hydrologic connectivity. I built on previous research by using

spatial patterns of dissolved organic matter to investigate coupling between terrestrial and aquatic C and nitrogen cycles. I estimated the separate and combined influence of five landscape components (lake area trends, soil characteristics, wildfire, and lake-specific traits) on water chemistry using random forest modeling and linear modeling. I then explored the implications for C and N dynamics by evaluating predictions derived from mechanistic hypotheses, and by comparing model results across organic and inorganic water chemistry variables that are regulated by different physical and biological processes. Finally, I related my findings to spatial patterns of water chemistry and land ownership in the Yukon Flats National Wildlife Refuge in northeastern Alaska, to illustrate how models of landscape influences on water chemistry can be used to inform management decisions related to high-latitude lakes and the services they provide.

Relative importance of landscape components as drivers of water chemistry

Each water chemistry parameter was predicted best by a combination of land cover and lake-specific variables, which supported the hypothesis that boreal lake water chemistry is influenced by the direct and indirect effects of multiple landscape context components. For C, N, and other ions, lake-specific characteristics related to bathymetry were consistently strong predictors regardless of fire history or the composition of the surrounding landscape, which indicated that water residence time and opportunities for in-site physical and biological processing were primary determinants of water chemistry. However, results also showed that terrestrial land cover influenced the chemical signature of boreal floodplain lakes through subsidies of inputs of dissolved organic material, and that changes in land cover may have been more important determinants of short-term lake ecosystem responses to warming than climate feedback mechanisms such as lake shrinkage, fire and permafrost thaw.

One of my most striking results was the association between lake depth and spatial patterns of C and N concentrations, an association that spanned several orders of magnitude (Fig. 3.5). Besides highlighting the extreme variation in lake chemical signatures and trophic states that can occur in boreal landscapes, this pattern also suggests that water chemistry is strongly regulated by physical characteristics of the lake basin regardless of the landscape context, including vegetation, soils, and disturbance history (Read et al. 2015). This result is consistent with large-scale studies of lake water chemistry in multiple ecoregions, including a recent examination of lake water chemistry drivers spanning the continental United States (Carpenter 1983; Rasmussen et al. 1989; Read et al. 2015). In previous work, depth-chemistry correlations have been linked to water residence time, which tends to be longer in deeper lakes (Hollister et al. 2011), and to the ratio of lake-bottom sediment area to lake volume. This ratio tends to increase with depth and facilitates chemical exchange between lake water and the surrounding substrate (Carpenter 1983). Both of these mechanisms may operate in the Yukon Flats and other boreal floodplain areas, but the strong correlation between depth and surface area/volume ratio across the sample population of lakes also suggested that depth effects may have been driven by evapo-concentration of nutrients and ions in shallow lakes. If residence time were the primary mechanism linking depth and water chemistry, I would have expected a substantially stronger effect on DOC than on DON or conductivity, since DOC is also susceptible to UV photo-degradation over time (Hudson et al. 2003). Moreover, total N has been linked to $\delta^{18}O$ signatures in other Yukon Flats lakes, which suggests that lake N levels are driven by evaporation/inflow ratio (Lewis et al 2014a). My data indicate that DOC concentrations are similarly affected by evaporation in flat-bottomed, shallow lakes.

Despite the clear conceptual link between lake shrinkage and depth, the evidence for chemical responses to drying in Yukon Flats lakes was subtle. Although lake change models had strong support for all response variables except DIN, only one lake change variable (Laketrend) was highly ranked in

terms of variable importance in any of the combined models (Fig. 3.3, Fig. 3.4), and its association with C, N, and ions was highly non-linear. The discrepancy between the predictive power of lake-change models and the variable importance scores for lake shrinkage indices may reflect the fact that lake shrinkage is only one of many factors influencing lake depth and evaporation rates, and cannot solely explain the existence of the shallowest lakes in the Yukon Flats landscape. Once the shallowest lakes (which had C and N values orders of magnitude above the mean) were removed from the dataset, shrinking lakes did show significantly elevated organic C and N levels relative to stable lakes, as has been observed for total N in previous research (Fig. 3.6; Lewis et al 2014a). The severity of chemical responses to shrinking may therefore depend on whether a lake has a shallow bathymetric profile and a close association between surface area and maximum depth (Carpenter 1983). More significantly, the importance of lake shrinkage as a landscape-level driver of water chemistry could increase dramatically if shrinking trends intensify and become a primary determinant of lake depth.

Although maximum depth, a lake-specific trait, was the strongest predictor of most water chemistry measurements, multi-model comparison indicated that land cover variables were more important. The structure and distribution of plant communities on boreal landscapes can shift rapidly due to the combined influence of climate, hydrology, and fire (Klein et al. 2005; Whitehouse and Bayley 2005; Balshi et al. 2007; Jonsson and Wardle 2010). However, despite their sometimes transient existence, boreal wetlands are highly productive, and the organic matter they produce can make up the majority of DOC inputs to adjacent surface waters (Gergel et al 1999). These C inputs make up a significant fraction of total C budgets in boreal landscapes, as boreal lakes typically have respiration rates much higher than GPP, and can annually release up to 20% of terrestrially produced C as CO_2 while also sequestering 10 times as much soil C per area as adjacent forests (Cole et al. 2007). Given the strength of the relationship between DOC and graminoid wetland size, this study provides

strong support for treating boreal terrestrial and freshwater C budgets as part of a single, integrated system (Cole et al 2007; Zhu and McGuire 2016).

Conceptually, the size of lake-margin graminoid wetlands should be associated with lake shrinkage, because retreating lake shorelines create new substrate for wetland plants to colonize (Klein et al 2005; Roach et al 2011). However, I was unable to detect this relationship in my data, and its effects may have been overwhelmed by other influences on the distribution of wetland plant communities, which could include disturbance history, topography, permafrost distribution, soil drainage, and precipitation patterns. Most of these factors are sensitive to climate, and continued high-latitude warming could influence the distribution of wetland plant communities through multiple pathways other than lake shrinkage (Whitehouse and Bayley 2005; Jonsson and Wardle 2010; Roach et al 2011).

Lake water chemistry was relatively insensitive to the distribution of permafrost and showed no relationship to fire history, a surprising result given that these are two of the most influential forces that shape boreal landscapes (Table 3.2; Fig. 3.3; Fig. 3.4). Permafrost is strongly associated with the existence of lake-dominated northern lowlands, since its presence precludes soil drainage and allows water to pool (Yoshikawa and Hinzman 2003), and fire is the main disturbance agent in boreal ecosystems, with demonstrated mechanistic effects on rates of lake shrinkage, soil organic C content, vegetation succession, and permafrost thaw (Balshi et al 2007; Jonsson and Wardle 2010; Roach et al 2013). Permafrost thaw due to fire and warming allows groundwater to move through deeper soil flow paths, and is typically thought to increase dissolved solute concentrations in groundwater (Lewis et al 2014b). However, in deep mineral soil layers, organic solutes are more likely to be mineralized and taken up by plant and soil microbes before reaching lakes, which could counteract the positive relationship between thaw and dissolved C and N concentrations (Neff et al 2003). Likewise, while fire appears to promote lake shrinkage, it also volatilizes massive amounts of organic C stored in adjacent

soils and terrestrial vegetation that would otherwise be available for export (Balshi et al. 2009). Finally, fire history data for Alaska is relatively coarse, and may not reflect the influence of wildfire on herbaceous wetlands, which have saturated soils and almost no woody fuel (Berg et al. 2009). In other words, the large adjacent wetlands associated with high in-lake DOC concentrations may also act as a buffer against fire effects on lake water chemistry. Lakes in the Yukon Flats have demonstrated high resilience to fire effects over 1-2 years (Lewis et al 2014b), and this study suggests that the lack of fire effects on water chemistry extends to decadal time-scales.

Landscape connectivity through lake-area change

Because lakes were sampled using a spatially balanced design, the number of shrinking and fluctuating lakes in my dataset was small relative to the number of stable lakes. While this distribution allowed for robust inferences about the relative importance of water chemistry drivers across the landscape (Stevens and Olsen 2004), it limited my ability to model the chemical signatures of shrinking and fluctuating lakes separately. Nevertheless, the data supported my hypothesis that lake area dynamics mediated the extent to which lakes were influenced by the surrounding landscape compared to internal processes.

Two clear patterns emerged from my comparative analysis of lake types. First, water chemistry variables were more strongly correlated with lake-specific variables (e.g. depth), but less strongly correlated with terrestrial land cover (e.g. graminoid wetland size), in shrinking lakes compared to stable lakes (Table 3.4). These relationships are consistent with the hypothesis that shrinking lakes are less hydrologically connected to the surrounding landscape, and that the chemical content of their waters is more strongly affected by internal processing than by external inputs (Fraterrigo and Downing 2008). Second, the chemical signature of flooding lakes was strongly associated with the size and distribution of other nearby lakes on the landscape (Table 3.4). Flooding lakes were the only subgroup

to show significant correlations with freshwater land cover variables (Table 3.4). This result supports my hypothesis that flooding patterns can be better determinants of a lake's surface hydrologic connectivity than traditional landscape position metrics based on the presence of input streams and drainage channels (Wantzen et al. 2008). Because estimates of lake area change are relatively straightforward to calculate using freely available remote-sensing data (Roach et al 2011; Rover et al 2012), these estimates could provide a cost-effective means of predicting the influence of landscape change on water chemistry in remote areas. Measures of shrinking and flooding frequency may become increasingly important to consider for high latitude lakes if warming alters seasonal precipitation patterns and affects the timing and severity of spring snowmelt and associated flooding.

Coupled responses of C, N, and other ions

Identifying the mechanisms behind spatial variation in point measurements of DOC or total N is difficult because *in-situ* measurements can be influenced by seasonally varying biological and physical processes, including uptake by microbes and phytoplankton (Stepanauskas et al. 2000; Spencer et al. 2008). However, the pronounced coupling of response variables led me to infer that in-lake biological uptake and processing had little effect on dissolved C and N concentrations, and that DON represented the majority of N inputs to Yukon Flats lakes.

I drew this conclusion by comparing the distribution and responses of DOC, total N, and DON. All three response variables were strongly associated with the distribution of conductivity values, which primarily reflect the concentration of conservative, biologically inert ions (Waiser 2006). If in-lake uptake was a prominent influence on DOC or DON measurements, I would have expected that these values would be more strongly associated with lake-specific variables versus land cover variables when compared with conductivity, which I did not observe (Waiser 2006; Lewis et al 2014a). Moreover, if lakes were receiving substantial groundwater inputs of nitrate and ammonium, which

were then rapidly taken up by lake biota, I would not have expected to see strong correspondence between conductivity (which represents inorganic ions) and organic C and N.

Because the majority of DON is not bioavailable for boreal lake primary production, most of this DON is used to support microbial respiration, which in turn facilitates the breakdown of DOC and production of CO_2 (Khalili et al. 2010). Large-scale studies of boreal lakes show that the ratio of DON to DIN inputs is positively correlated with the ratio of C evasion vs. accumulation, with up to 87% of DOC inputs being respired in the highest-DON lakes (Khalili et al. 2010). Additionally, humic peat-derived organic matter, which represents the primary source for organic C and N inputs in boreal systems, tends to suppress primary production by reducing light penetration (Schindler et al. 1997). Coupled terrestrially derived DOC/DON inputs can therefore simultaneously suppress primary production while amplifying respiration rates, which suggests that graminoid land cover and other factors driving those inputs could be important predictors of net C flux between lakes, lake sediments, and the atmosphere.

Management Implications

Water chemistry metrics varied by several orders of magnitude across the lowland floodplain area of the Yukon Flats National Wildlife Refuge (Fig. 3.7). The spatial distribution of nutrient concentrations were significantly lower on privately held lands within the Refuge, including villages owned by local Native corporations, than on adjacent federal holdings (Fig. 3.8). The implications of spatial water chemistry variation for wildlife/waterfowl habitat, which is the primary management objective on Refuge lands, were ambiguous, since lake food webs in the Yukon Flats appear unresponsive to long-term changes in nutrient and ion concentrations (Lewis et al. 2014b), and current spatial patterns in waterfowl richness are only weakly correlated with lake conductivity (Roach and Griffith 2015). The median total N concentration in lakes on federally owned land exceeded a published threshold for hyper-eutrophic status (Fig. 3.8), suggesting impaired water quality, and a

potential need for land exchanges to protect areas with deep, relatively oligotrophic lakes. However, the most 'impaired' lakes in the study area were also those apparently receiving the largest inputs of terrestrial C (Fig. 3.5). Traditional water quality metrics based on lake trophic state (e.g. eutrophic vs. oligotrophic) are therefore potentially misleading, since they do not reflect the value of all ecosystem functions provided by boreal lakes, which include C storage, and the current DOC bias between privately and federally owned lakes in the YFNWR may actually be appropriate given the needs of local residents for access to clean water, and the public benefits derived from protecting areas of high C storage potential.

Conclusions

I found that lake size dynamics were a minor influence on summer water chemistry and dissolved organic C inputs in lakes of the Yukon River Basin. However, the chemical signatures of lakes in this region were closely tied to bathymetry, and continued widespread lake shrinkage at high latitudes has the potential to significantly affect the concentration of dissolved C, nutrients, and other ions by altering the distribution of lake depths at local and regional scales. Inter-annual variation in lake size may also be an important driver of hydrologic and chemical connectivity between boreal lakes, and should be considered when estimating the consequences of warming-driven changes in precipitation patterns and spring melt on lake ecosystems.

This study provides landscape-level evidence of terrestrial-freshwater lake interactions, including flooding and lake shrinkage, as important feedbacks between climate change and C cycling in boreal lowlands. I examined the factors that control such interactions, and identified the distribution of nearshore wetland vegetation and lake bathymetry as two important predictors of boreal lake chemistry. This information could be used to improve assessments of water quality and C storage in lake-dominated Alaskan landscapes, and to guide future efforts to model terrestrial and aquatic C

dynamics at high latitudes. Accurately accounting for the coupled nature of terrestrial and freshwater C dynamics is essential for understanding the current and future C-sink strength of boreal lowlands, which are characterized by a mosaic of organic C-rich peat and abundant lakes.

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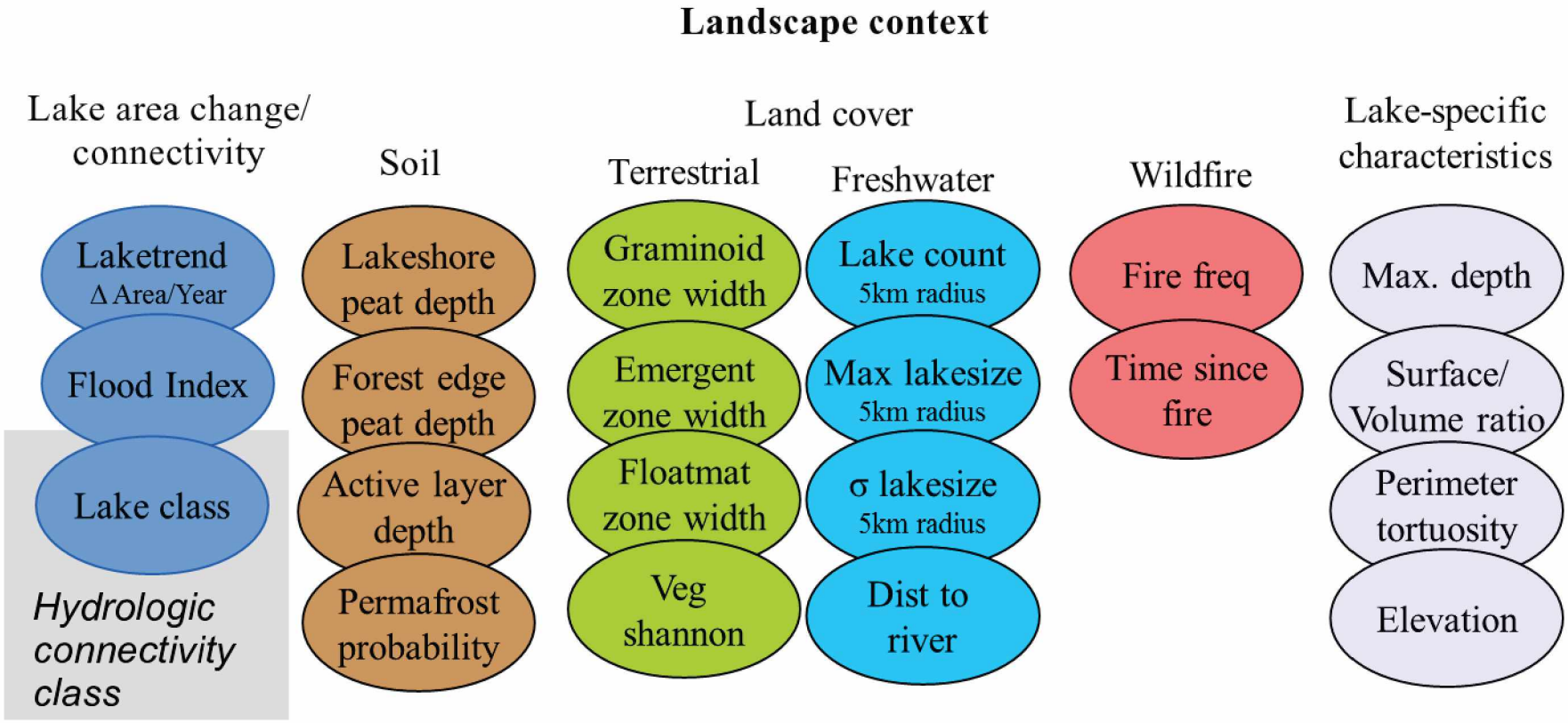

Figure 3.1. Landscape context conceptual diagram. This diagram links five classes of water chemistry drivers (Lake-area change, soil properties, land cover, wildfire, and lake-specific characteristics) with specific predictor variables. Variables related to lake size variability can be represented as a separate class of landscape disturbance, or as hydrologic connectivity variables. Modified with permission from Read et al. (2015).

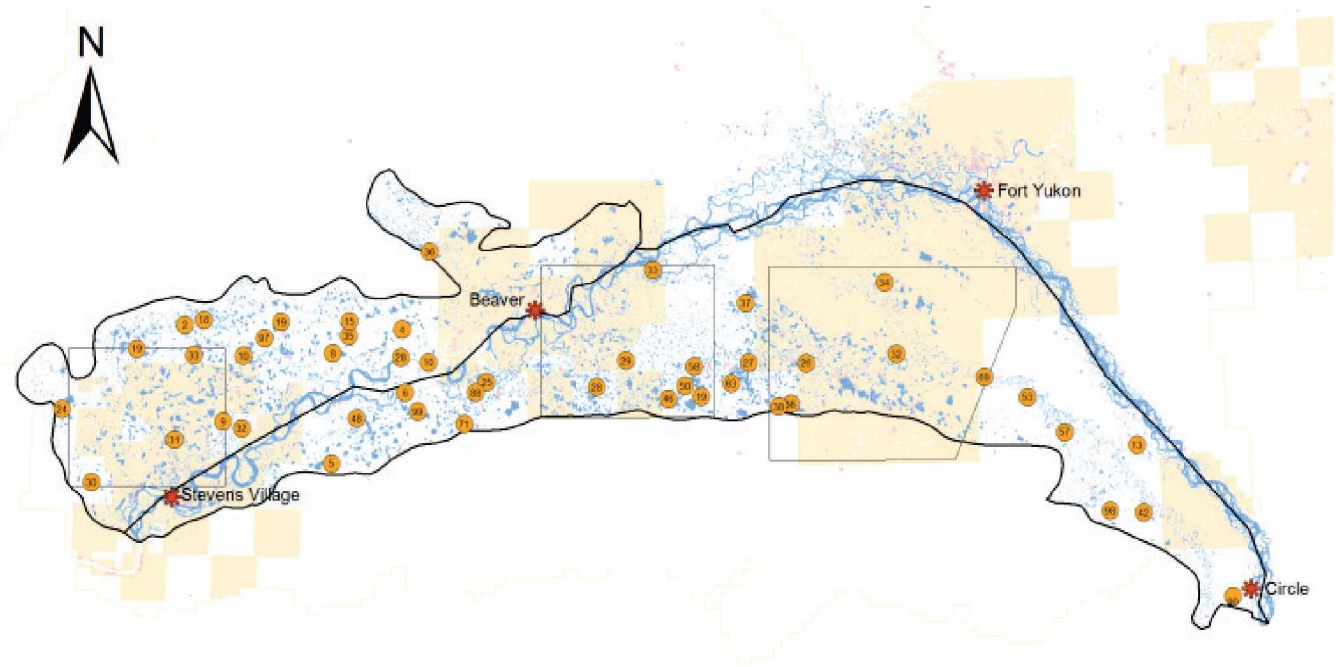

Figure 3.2. Study area. Overview map of study area in the Yukon Flats National Wildlife Refuge, Alaska. The two sample strata are outlined in black, focal sites are marked in yellow, and villages are shown in red. Shaded polygons show the location of private and Native Corporation land.

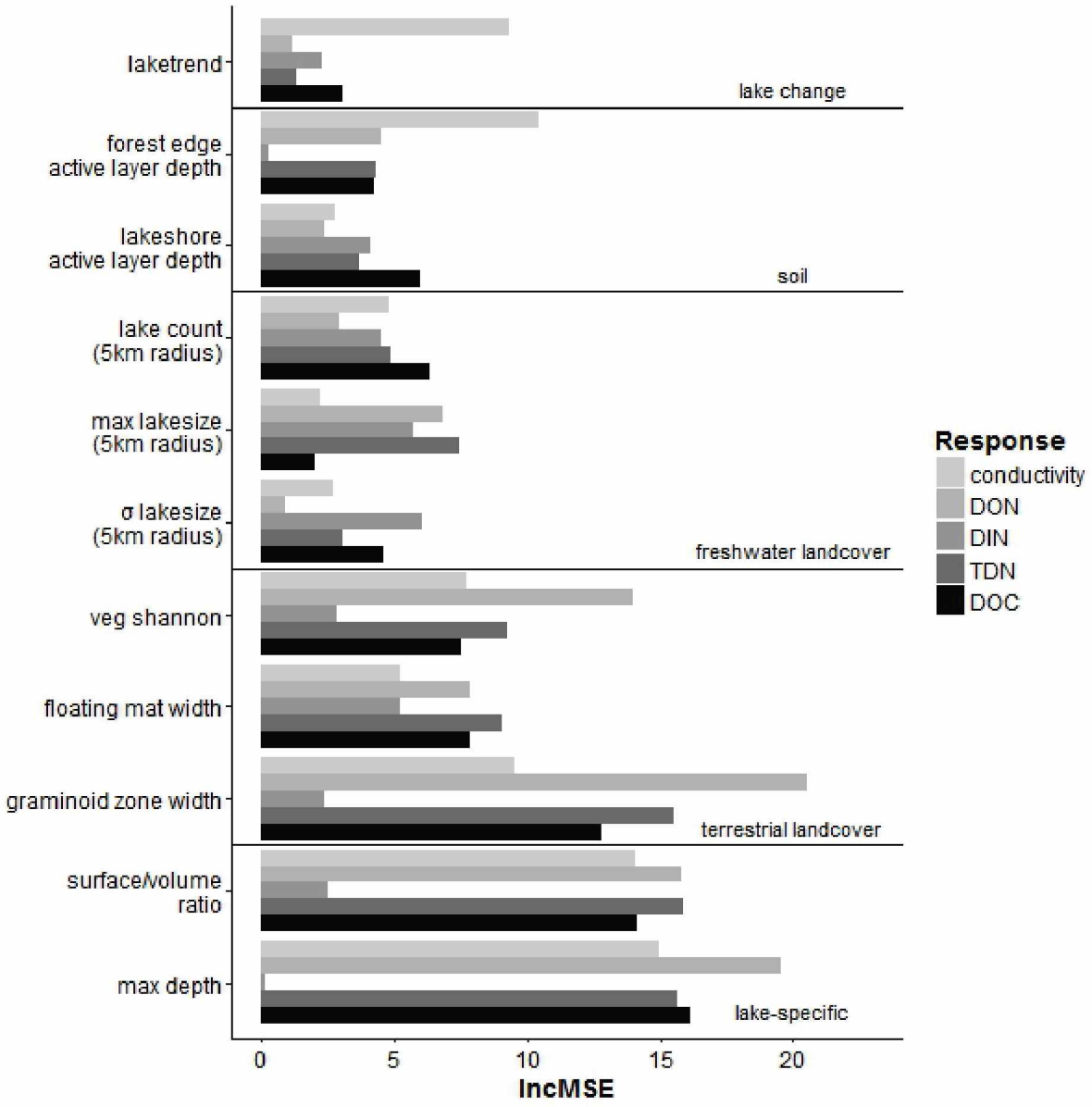

Figure 3.3. Water chemistry variable importance. Variable importance plots for combined random forest models of summer lake water chemistry measurements in the Yukon Flats National Wildlife Refuge. Variable importance scores represent the average increase in model mean squared error (IncMSE) when the values for a single predictor are randomly permuted. Scores are shown for all predictors that were one of the top five importance scores for at least one response variable. Response variables were conductivity, dissolved organic nitrogen (DON), dissolved inorganic nitrogen (DIN), total dissolved nitrogen (TDN), and dissolved organic carbon (DOC). Table 3.1 contains a complete list of all predictor variables used and their abbreviations.

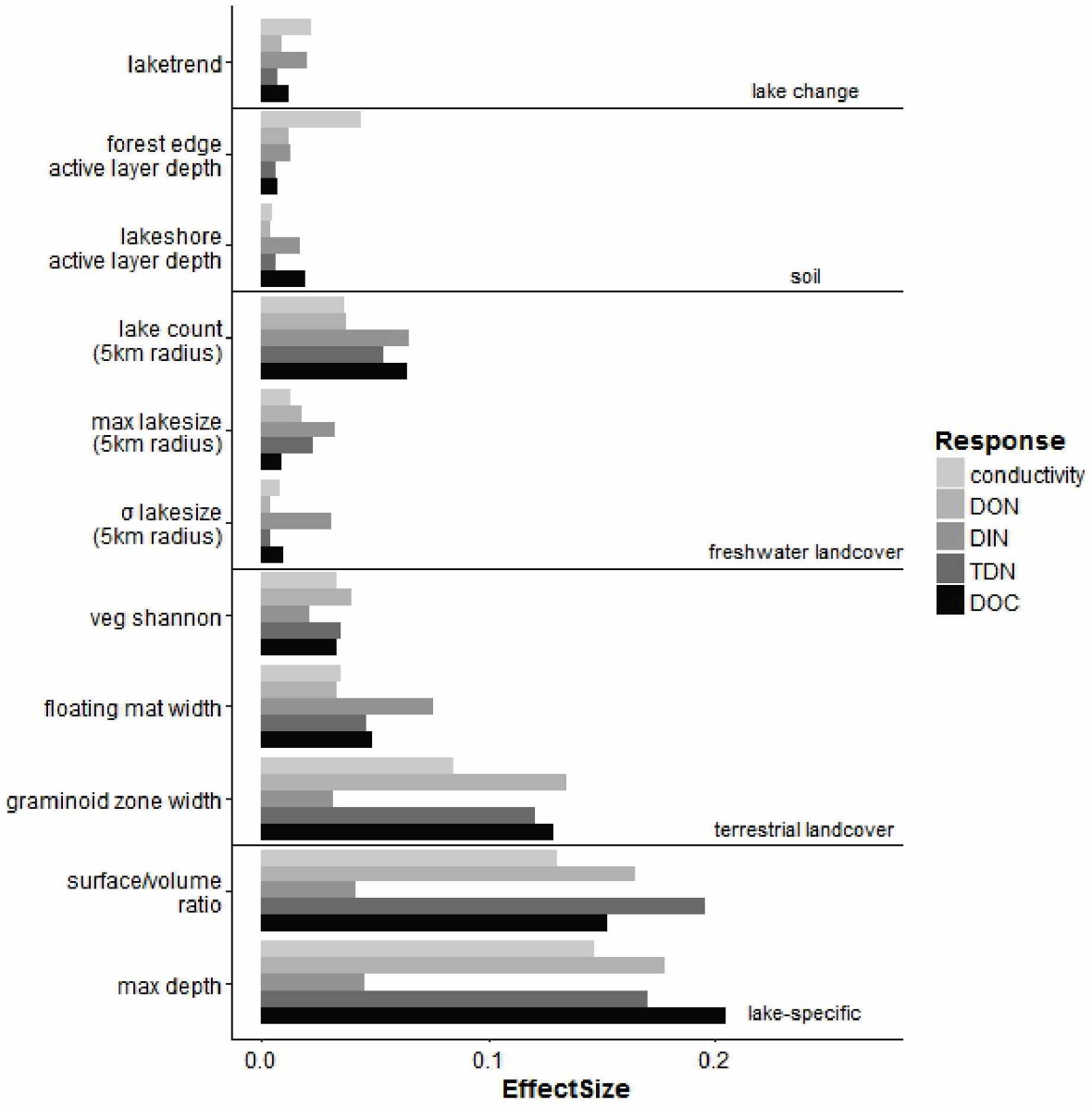

Figure 3.4. Water chemistry variable effect size. Variable effect size estimates for random forest models of summer lake water chemistry measurements in the Yukon Flats National Wildlife Refuge. Effect size indices were derived from partial dependence plots which depict the average response of water chemistry measurements to single predictor variables while accounting for the influence of all other predictors in the model. Effect size was calculated as the y-axis range from each partial dependence plot divided by the observed range of response variable values, and are heuristically similar to the absolute value of slope estimates from ordinary linear regression models. Response variables were conductivity, dissolved organic nitrogen (DON), dissolved inorganic nitrogen (DIN), total dissolved nitrogen (TDN), and dissolved organic carbon (DOC). Table 3.1 contains a complete list of all predictor variables used and their abbreviations.

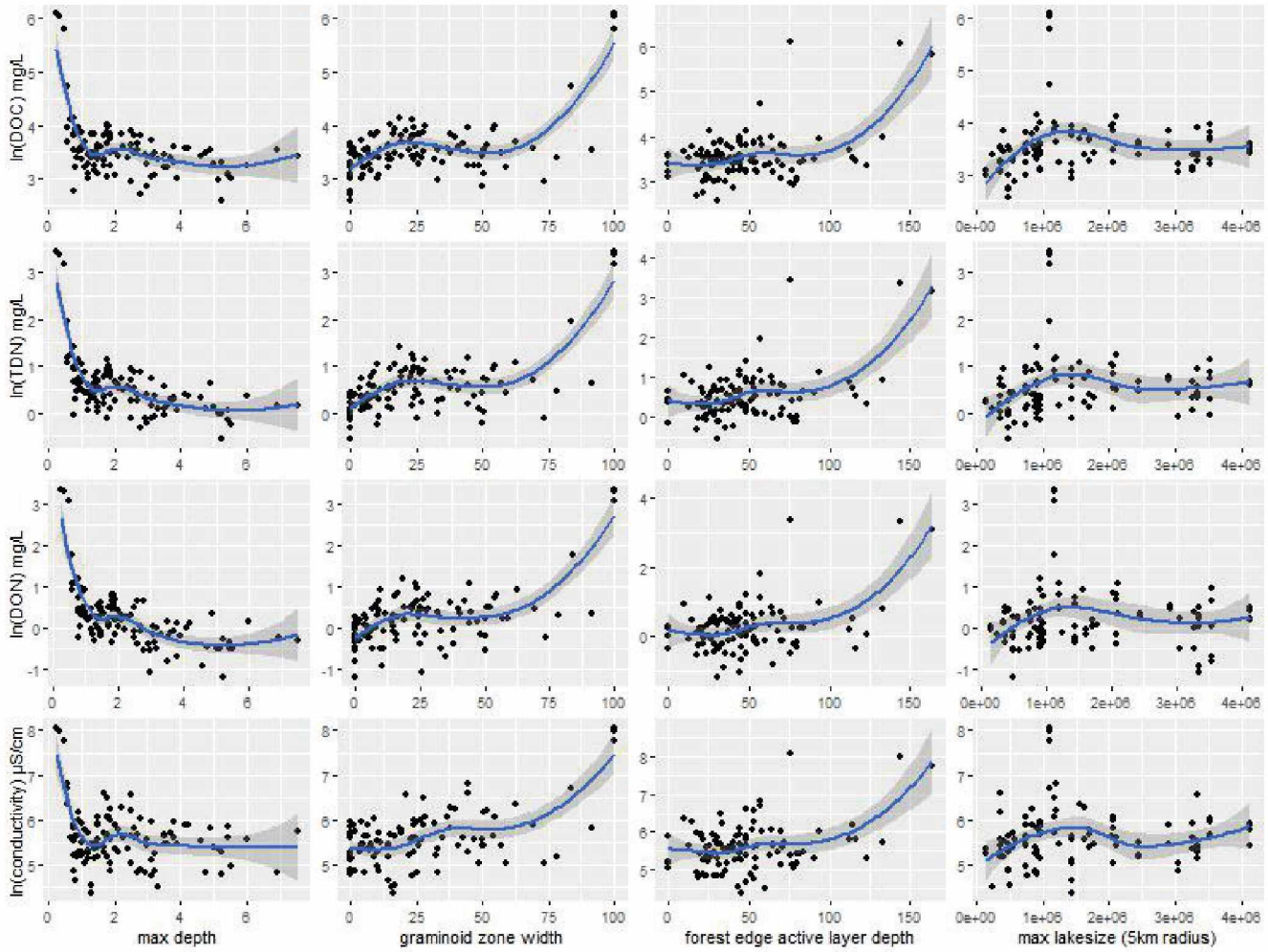

Figure 3.5. Water chemistry scatterplots. Predicted values for water chemistry measurements from lakes in the Yukon Flats National Wildlife Refuge, plotted against top-ranked predictor variables from random forest models based on lake-specific, terrestrial land cover, soil, and freshwater land cover variables (see Table 3.1). Response values are log-transformed. Panels show estimates for individual lakes, with loess-fitted smooth curves and associated 95% confidence intervals for those curves.

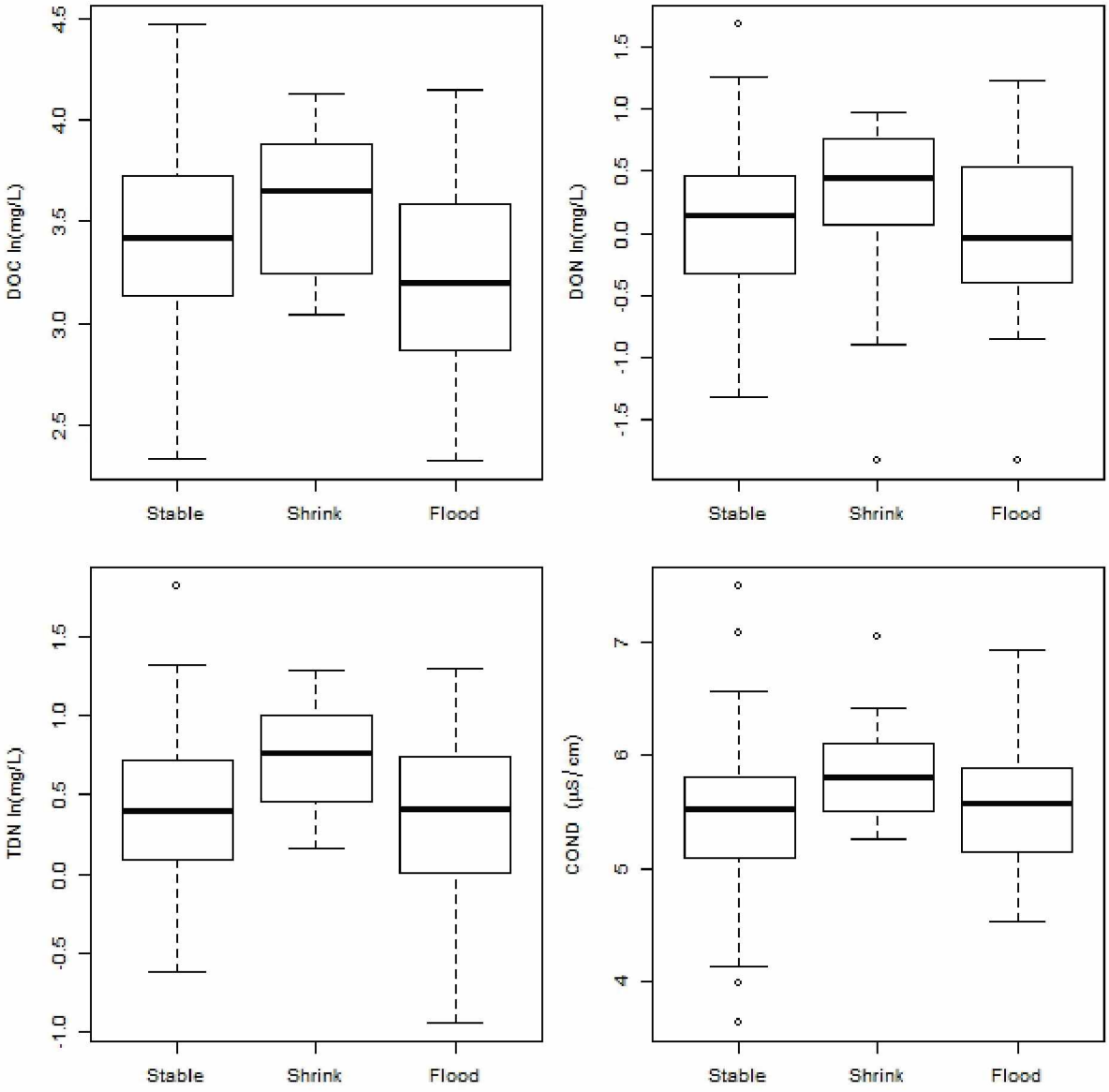

Figure 3.6. Water chemistry variation by lake class. Boxplots of lake water chemistry measurements as a function of lake classification (stable, shrinking, or flooding) after four outlier lakes from a single focal site have been removed from the dataset. When the four lakes with the highest C, N, and conductivity values were removed, lake type was a significant predictor of total dissolved nitrogen (TDN; $F=3.719$, $df=2,92$, $p=0.047$) and conductivity ($F=3.46$, $df=2,92$, $p=0.035$), but not dissolved organic carbon (DOC; $F=2.53$, $df=2,92$, $p=0.085$) or dissolved organic nitrogen (DON; $F=0.79$, $df=2,92$, $p=0.45$). All response variables were log-transformed prior to analysis.

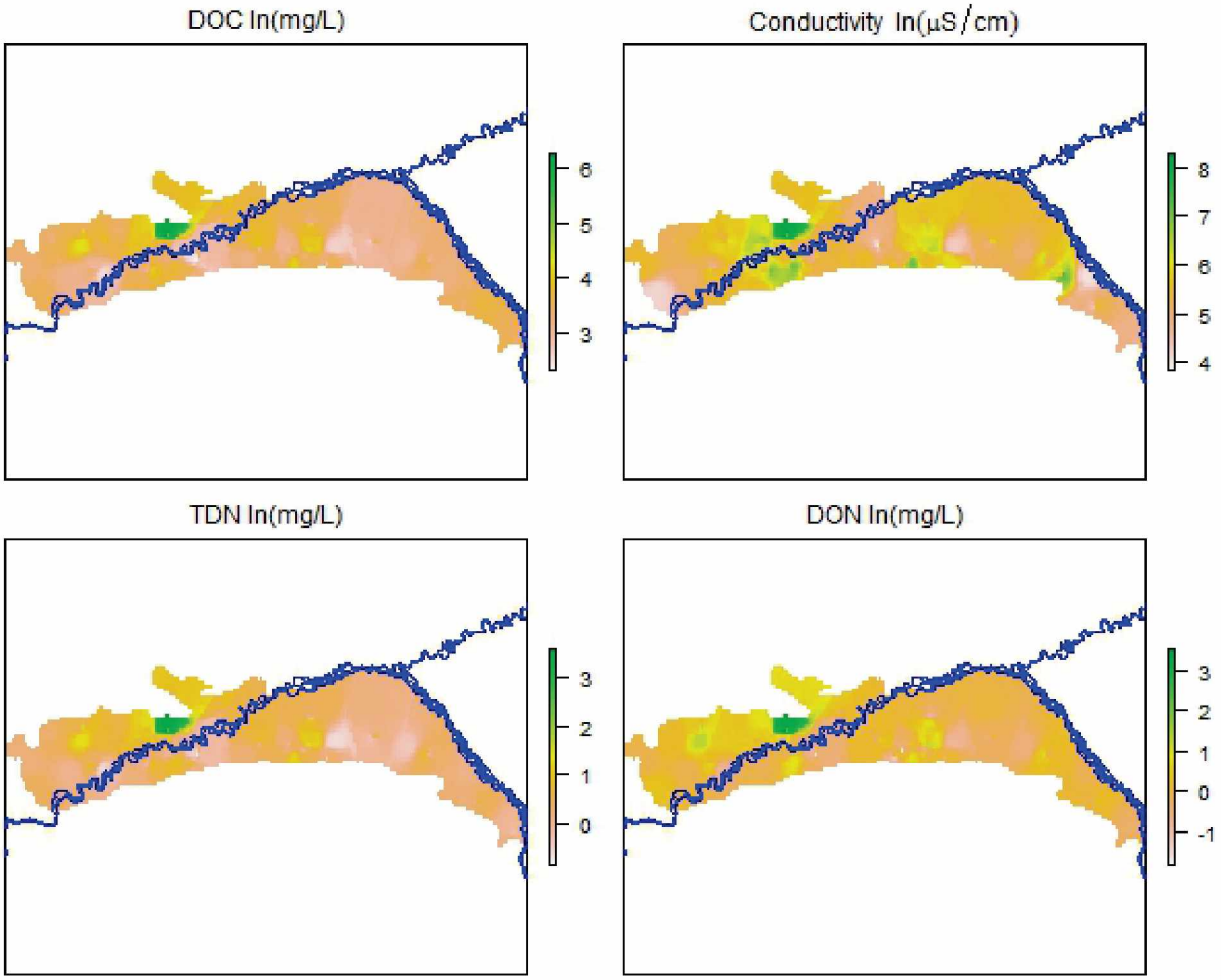

Figure 3.7. Yukon Flats water chemistry surface maps. Spatially interpolated estimates of water chemistry variables in the Yukon Flats National Wildlife Refuge, Alaska. Values were interpolated from a spatially balanced random sample of 130 lakes using inverse distance weighting with an inverse distance weighting power of 2 and 5 nearest neighbors. Optimal parameter values were identified using 10-folds cross-validation. Cross-validated predictive power (R^2 for regression models of predicted values ~ observed values) = 0.55 for DOC, 0.53 for TDN, 0.44 for DON, and 0.38 for conductivity. Blue lines show the location of the Yukon and Porcupine rivers. Map resolution (pixel size) is 1 km^2.

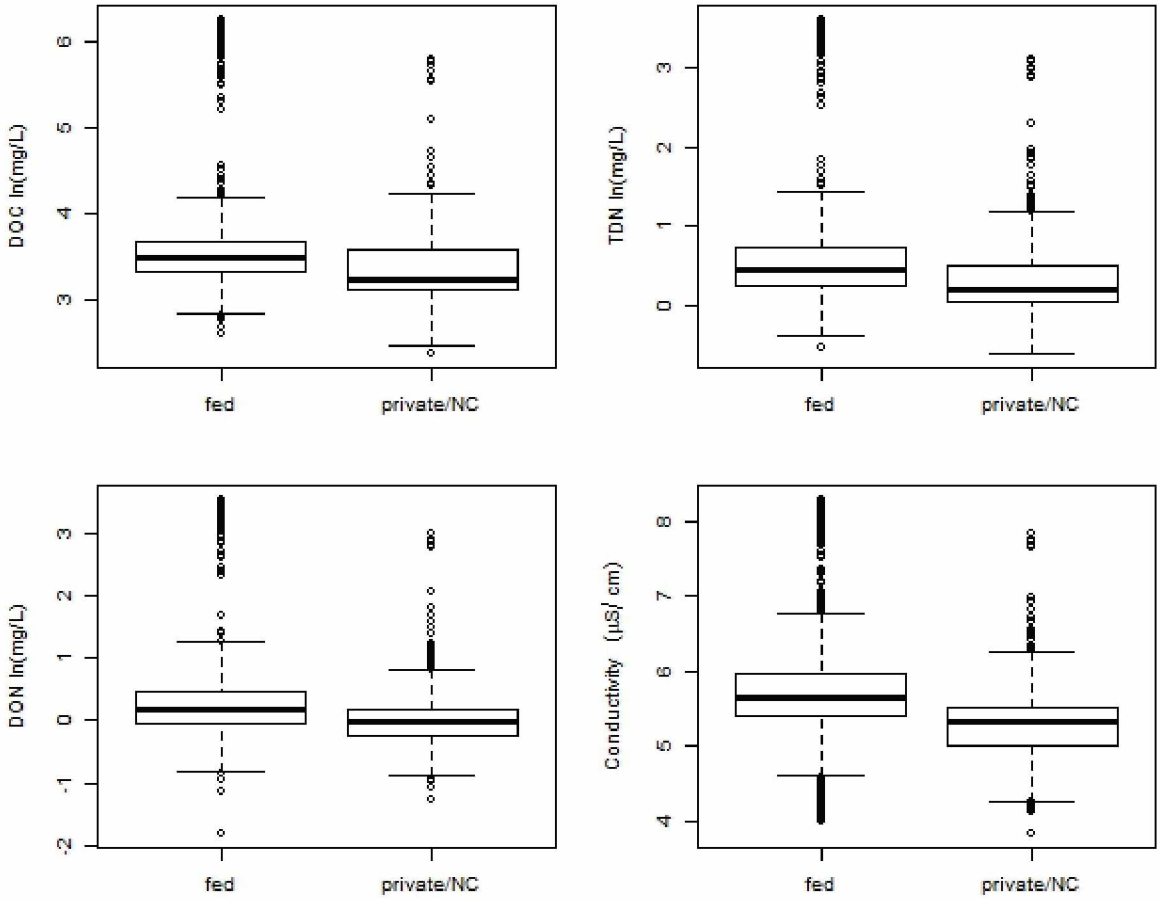

Figure 3.8. Water chemistry measurement boxplots. Values were interpolated from inverse distance weighting maps derived using point measurements from 130 lakes in the Yukon Flats National Wildlife Refuge. Boxes show the median, 25th, and 75th percentile of interpolated values from map pixels representing federal land (fed), and private/Native Corporation holdings (private/NC). The effect of landownership was highly significant for all water chemistry variables based on one-way ANOVA.

Table 3.1. Random forest model variables. Model and predictor variable descriptions for random forest analysis of lake water chemistry variation in the Yukon Flats National Wildlife Refuge, Alaska.

Model	Predictor Variable	Data source
All models	Julian Day (Days since Jan 1)	This study
Lake Change	Laketrend (annual rate of change in surface area; ln(m^2/year)	This study/Rover et al. 2012
	Flood index	This study/Rover et al. 2012
	Lake class	This study/Rover et al. 2012
	Shrinking	This study/Rover et al. 2012
	Flooding	This study/Rover et al. 2012
Wildfire	Fire freq (number of fire scars < 50 years old that cover a lake)	afs.ak.blm.gov
	Years since fire (<10,10-25,25-50,>50)	afs.ak.blm.gov
	Burned within 10 years	afs.ak.blm.gov
	Burned within 25 years	afs.ak.blm.gov
	Burned within 50 years	afs.ak.blm.gov
Soil	Lakeshore peat depth (cm)	This study
	Forest edge peat depth (cm)	This study
	Lakeshore active layer thickness (field measurement; cm)	This study
	Forest edge active layer thickness (field measurement; cm)	This study
	Active layer thickness (cm)	Pastick et al. 2013
	Permafrost probability	Pastick et al. 2013
Terrestrial land cover	Graminoid zone width (m)	This study
	Emergent zone width (m)	This study
	Floating mat zone width (m)	This study
	Veg shannon (Plant community shannon diversity index)	This study
Freshwater land cover	Lake count (5km radius)	This study
	Max lakesize (5km radius)	nhd.usgs.gov
	Mean lakesize (5km radius)	nhd.usgs.gov
	σ lakesize (5km radius)	nhd.usgs.gov
	Dist to river (Distance to major rivers; km)	nhd.usgs.gov
	Dist to stream (Distance to any stream or river; km)	nhd.usgs.gov
Lake-specific	Max depth (m)	This study
	Surface area (ha)	This study
	Perimeter tortuosity (Shoreline / Perimeter of equal-area circle)	This study
	Surface/Volume ratio	This study
	Elevation (m)	This study

Table 3.2. Random forest model performance. Model performance shown as the fraction of variance explained for alternative random forest regression tree models of spatial variation in summer lake water chemistry, Yukon Flats National Wildlife Refuge. Response variables were dissolved organic carbon (DOC), total dissolved nitrogen (TDN), dissolved inorganic nitrogen (DIN), dissolved organic nitrogen (DON), and conductivity. Each column represents the fit for a model representing a hypothetical class of driving variables (Table 3.1). The combined model included all predictor variables from each sub-model, while the combined top five models used only those predictors with the five highest variable importance scores for each response. Response values were log-transformed prior to analysis to meet assumptions of normality.

	Lake Change	**Wildfire**	**Soil**	**Terrestrial land cover**	**Freshwater land cover**	**Lake Specific**	**Combined**	**Combined Top Five**
DOC	0.41	-0.07	0.4	0.39	0.35	0.22	0.49	0.52
TDN	0.41	-0.06	0.39	0.38	0.4	0.26	0.54	0.54
DIN	-0.15	-0.07	0.01	-0.1	-0.13	-0.09	-0.07	0.03
DON	0.35	-0.03	0.34	0.33	0.42	0.23	0.57	0.54
conductivity	0.35	-0.06	0.25	0.33	0.26	0.13	0.37	0.38

Table 3.3. Yukon Flats lake type distribution. Comparison of lake classifications between Yukon River Basin project study lakes and the Yukon Flats National Wildlife Refuge overall. Large-scale analyses used lake area time series for all Landsat-detectable lakes in the central 2/3 of the Yukon Flats (n=13269). Time series data were provided by Dr. Jennifer Rover, USGS. Lakes were categorized as Stable, Shrinking, or Flooding in both samples based on linear regression using Landsat imagery obtained between 1980 and 2011.

Sample	Stable	Shrinking	Flooding	Total
YRB study lakes	71 (0.68)	18 (0.17)	19 (0.18)	108
Central Yukon Flats	10463 (0.79)	754 (0.06)	2052 (0.15)	13269

Table 3.4. Water chemistry drivers by lake type. Correlations between water chemistry measurements and top-ranked driver variables from lake-specific, terrestrial land cover, freshwater land cover, and soil models, stratified by lake type. Numbers represent Pearson correlation coefficients. * = significance at alpha = 0.1, and bold text with ** = significance at alpha = 0.05. Lake types were shrinking (shrink; n=18), flooding (flood; n=19), and stable (n=71).

Response	Lake Type	max depth	graminoid zone width	max lake size (5km radius)	forest edge active layer thickness
DOC	shrink	-0.43*	0.08	0.03	0.29
DOC	flood	-0.33	0.12	**0.53****	0.38
DOC	stable	**-0.27****	**0.58****	-0.08	**0.4****
TDN	shrink	**-0.6****	0.31	-0.01	0.29
TDN	flood	-0.39	0.18	**0.59****	0.35
TDN	stable	**-0.27****	**0.57****	-0.07	**0.39****
DON	shrink	**-0.52****	0.3	-0.24	0.24
DON	flood	-0.4*	0.13	**0.58****	0.41
DON	stable	**-0.27****	**0.56****	-0.08	**0.38****
Conductivity	shrink	-0.27	0.35	-0.06	-0.04
Conductivity	flood	-0.16	0.23	0.31	0.17
Conductivity	stable	**-0.24****	**0.58****	-0.09	**0.38****

Chapter 4 : Projected landscape-scale effects of boreal lake area change[1]

Abstract

Long-term climate-mediated reductions in surface area of lakes, and increased inter-annual variability in lake size, have been detected throughout the boreal ecoregion in Alaska. These changes may influence the structure and function of adjacent wetland plant communities due to strong hydrologic connectivity between individual lakes and wetlands. However, lakes occupy only a small fraction of the landscape, and the majority of boreal lakes have not significantly increased or decreased in size over time. This heterogeneity must be accounted for when determining the landscape-level implications of lake shrinkage. I used space-for-time substitution to project past and future changes in lake size, wetland size, and wetland characteristics (above-ground biomass and plant functional divergence). Projections were driven by a set of simple empirically derived statistical models within a multi-stage Monte Carlo simulation framework, and were based on observed lake size dynamics in three sub-regions the Yukon Flats National Wildlife Refuge. Projections showed that the most rapid lake shrinkage rates that have currently been described could lead to order-of-magnitude reductions in total wetland surface area, as well as a shift towards increasingly shrub-dominated wetland plant communities. These changes have contradictory management implications for waterfowl species richness, which is expected to decrease as herbaceous wetlands shrink, and for moose, which could benefit from local increases in woody browse availability. Results also suggested that lake sediment carbon stocks are vulnerable to aerobic decomposition, and that sustained rates of lake shrinkage could significantly alter the carbon budgets of boreal lowlands. Overall, these models

[1] Patil, V. P., D. B. Griffith, S. E. Euskirchen, A. D. McGuire, and M. P. Waldrop. Projected landscape-scale effects of boreal lake area change. Prepared for Global Change Biology.

supported the hypothesis that reductions in the surface area of a small fraction of boreal lakes could have landscape-level effects on biodiversity, wildlife habitat, and carbon storage.

Introduction

Lakes and wetlands are dominant features of boreal Alaskan landscapes, due to the presence of poorly drained frozen soils, but are potentially vulnerable to the effects of climate change (Roach et al. 2011). Sustained high-latitude warming has led to the thawing of shallow permafrost (soil that is colder than 0 C for two or more years) and shifted the balance between recharge, drainage, and evaporation of lake water (Yoshikawa and Hinzman 2003; Walvoord and Striegl 2007; Romanovsky et al. 2010). These changes have caused lakes to shrink throughout the circumpolar Arctic and sub-Arctic over the last 50 years (Klein et al. 2005, Smith et al. 2005, Riordan et al. 2006, Rover et al. 2012). Lake shrinkage is widespread and rapid in Alaska. A recent study of lakes in eight National Wildlife Refuges distributed throughout the state found that approximately 10% of boreal lakes have shrunk significantly since 1980, and the same study projected an average loss of 24.7% of lake surface area over the next 50 years (Roach et al. 2013). At the same time, many lakes that appeared stable over the last few decades have experienced large inter-annual and seasonal fluctuations in surface area (Roach et al. 2013, Rover et al. 2012). As discussed in Chapters 2 and 3, inter-annual and inter-lake variability in lake size have generally been much greater than the average magnitude of decadal-scale trends. In addition to rapid warming, high latitudes are projected to experience an increase in the frequency and magnitude of extreme precipitation events (Sillmann et al. 2013), which suggests that climate change could simultaneously accelerate lake shrinkage while also amplifying fluctuations in lake surface area.

Boreal lakes are commonly surrounded by concentric rings of grass/sedge-dominated (GS) and woody shrub-dominated (SH) wetland vegetation (Whitehouse and Bayley 2005). These community types are hydrologically linked to lakes (Roach et al. 2011), and their size and distribution can be affected by lake dynamics (see Chapter 2). Drying lake margins expose bare sediment for colonization by herbaceous plant species, while reduced soil moisture can facilitate the encroachment of woody shrub vegetation into herbaceous fens through succession (Klein et al. 2005). At the same time, wetland expansion can cause further lake shrinkage by filling lake margins with peat-forming vegetation in a process known as terrestrialization (Roach et al. 2011). The net effect of these successional processes could be either an increase or decrease in the total area covered by woody and herbaceous wetlands, depending on the rate at which each community tracks the retreating shoreline of shrinking lakes. Flooding (lake size fluctuations) can also reset the successional stage of lake-margin communities, primarily by causing high mortality in woody shrub and tree species (Timoney et al. 1997, Asada et al. 2005), while encouraging the expansion of flood-tolerant species, particularly graminoids with aerenchymatous roots (Chapin et al. 1996, Larmola et al. 2004).

Changes in the size of lakes and wetlands could affect the ecological and social value of boreal landscapes, with complex implications for how those landscapes are managed in the face of continued warming and lake shrinkage. As herbaceous wetlands shrink, for example, plant diversity and the density of above-ground biomass (AGB) tend to increase, but these trends are associated with edge effects and increased abundance of woody shrubs (Chapter 2). Wetland size is inversely correlated with plant functional trait diversity (Chapter 2), and increased functional diversity could promote resilience in shrinking wetlands and help buffer against rapidly changing disturbance regimes (Sandra and Cabido 2001). However, boreal lakes and herbaceous (i.e. non-

woody) wetlands are breeding habitat for millions of migratory birds and other wildlife (Riordan et al. 2006, Roach and Griffith 2015). Their loss or shrinkage could reduce local waterfowl diversity over the next 50-100 years (Roach and Griffith 2015), and other wildlife species could be similarly affected.

The widespread shrinking of boreal lakes and wetlands may also affect regional and global C budgets, because boreal lakes and wetlands store a disproportionately large fraction of all boreal organic C (Kortelainen et al. 2004, Benoy et al. 2007, Cole et al. 2007). Lake C stocks in particular could be rapidly lost as shrinking lakes are replaced by terrestrial vegetation, because limnic sediments are vulnerable to rapid aerobic decomposition and microbial respiration (Jorgenson et al. 2013). There has been little research on lake drying's implications for C storage in boreal Alaska, due to the limited availability of lake soil C data and the difficulty involved in estimating rates of lake area change (Zhu and McGuire 2016). However, extensive field studies in Scandanavia suggest that boreal C stocks are strongly associated with the sizes of individual lakes and wetlands (Kortelainen et al. 2004).

While lakes and wetlands occupy a small fraction of most boreal landscapes (Kortelainen et al. 2004, Rover et al. 2012), the ecological ramifications associated with changes in lake surface area may be substantial. However, the ecological significance of lake size dynamics cannot be properly assessed without scaling up from the responses of individual lakes and wetlands to the landscape as a whole. There are several options available for estimating the ecological effects of lake shrinkage on wetland plant communities, each with its own strengths and weaknesses. These include manipulative experiments, simulation modeling, long-term monitoring, and space-for-time substitution.

Manipulative experiments provide strong tests of specific mechanisms driving changes in ecosystem productivity, C storage, and other characteristics. However, it is rarely practical to manipulate variables such as temperature or precipitation at large spatial or temporal scales, and the results of short-term, localized experiments cannot always be confidently extrapolated (Rastetter et al. 1996). Mechanistic process-based ecosystem models can provide a solution to this problem, by integrating complex interactions between ecosystem components into a single, logically consistent framework. Such models provide insight into the mechanisms driving simulated change, and can reveal emergent long-term ecosystem properties, such as the decoupling of nitrogen and light competition that occurs when forested communities reach canopy closure (Rastetter et al. 1996). However, despite significant recent advances in dynamic vegetation modeling (e.g. Euskirchen et al. 2009), fine-scale spatial heterogeneity due to shifts in vegetation structure and land cover still present a significant modeling challenge (Hibbard et al. 2003; Wullschleger et al. 2014).

Land cover change can be incorporated into biogeochemistry models by combining rule-based or probabilistic transitions between land cover types with process-based models of ecosystem function (Hibbard et al. 2003). Given enough time, transition probabilities between land cover types can be estimated by monitoring long-term study plots. With modern remote sensing technology, estimates of land cover change can be estimated retroactively in many instances, by deriving a historical land cover time series through the interpretation of aerial photography and/or spectral reflectance data. Historical time series can then be used to derive rule-based or statistical models of land cover transition rates (e.g. Klein et al. 2005; Sulman et al. 2012), which can be used to project future vegetation change. This approach has been successfully used to estimate historical rates of lake area change throughout Alaska, because

open water is relatively easy to distinguish from land using multispectral data (Roach et al. 2011; Roach et al. 2013).

Unfortunately, boreal lowland plant communities with sparse yet multi-layered canopies are difficult to map accurately using spectral reflectance data (Lara et al. 2015). Some historical vegetation maps based on aerial photography, such as the National Wetlands Inventory (NWI), have high reported overall accuracy (Wilen et al. 1995). However, the NWI provides only a single map of Alaskan land cover by lakes, wetlands, and rivers, which was based on imagery obtained between 1980 and 1985. Moreover, the NWI has not been validated against contemporaneously collected field data to assess its accuracy in lowland boreal landscapes. Similar issues face other large-scale maps of boreal land cover, such as the National Land Cover Database (NLCD; www.nlcd.org).

In the absence of historical observations, space-for-time substitution models can provide a powerful tool for inferring the effects of historical ecological processes. The most common form of space-for-time substitution uses a chronosequence of vegetation patches that differ in age to understand successional dynamics over time (Walker et al. 2010). This approach is a plausible option for modeling the effects of lake shrinkage on wetlands, because the age of lake-margin wetlands should be positively correlated with distance from the shoreline of rapidly shrinking lakes. However, in landscapes where current spatial patterns of vegetation are tightly coupled with current environmental gradients (elevation, climate, and soil moisture/water table), chronosequences can fail to capture temporal vegetation dynamics, and space-for-time substitution across a toposequence or environmental gradient may be more appropriate (Walker et al. 2010). For example, elevational toposequences have been used to project the effects of

climate change on biodiversity (Blois et al. 2013), and vegetation type-water table associations have been used to model the effects of drying on peatland C dynamics (Sulman et al. 2012).

Bands of wetland vegetation can be found surrounding boreal lakes that have not shrunk or expanded in decades, suggesting that wetlands are not simply a transient successional stage on the path to a climax spruce forest community (Patil et al. unpublished data). Instead, these vegetation types are consistently distributed along a gradient of soil moisture, which is significantly higher near lakes than in the surrounding upland forest (Whitehouse and Bayley 2005; Jorgenson et al. 2013). If associations between the distribution of wetland vegetation, soil moisture, and proximity to lake-shore are sufficiently strong, the size of lakes and the size of lake-margin wetlands should be significantly correlated, and the effect of long-term lake shrinkage on future wetland size could be extrapolated by contrasting the wetland size distributions associated with large and small lakes.

In this study, I examine the implications of long-term change in lake surface area for the central lowlands of the Yukon Flats National Wildlife Refuge (YFNWR) in northern Alaska (Fig. 4.1). I hypothesized that lake size dynamics influence the size of lake-margin wetlands, as well as the biodiversity and abundance (AGB) of wetland plant communities, and below-ground C storage. I also hypothesized that if observed lake size changes continue, they could alter land cover, biodiversity, AGB, and C storage at the landscape scale over the next 100 years. I addressed these hypotheses with six objectives (Figure 4.2):

1) Use linear models to estimate historical trends and variability in lake size, and test for statistical relationships among lake size, lake shrinkage rates, wetland size, and wetland

characteristics (AGB and biodiversity). I fit these models using field measurements from a spatially balanced random sample of lakes from the YFNWR (Stevens and Olsen 2004).

2) Use the statistical relationships from objective 1 to project historical change in median lake and wetland area between 1986 and 2010, using a space-for-time approach (Roach and Griffith 2015). Projections encompassed three zones in the study area that were characterized by a) a small but significant increasing trend in lake size (west zone), b) a rapid, significant decreasing trend (central zone), and c) no significant lake size trend due to high inter-annual and intra-annual variability (east zone; Roach et al. 2013; Fig. 4.1). I explicitly contrasted projections between the west and central zones, and between the west and east zones, to infer the effects of lake trend (positive vs. negative) and lake size variance around that trend (low vs. high), respectively.

3) Verify that historical projections were consistent with other estimates of lake and wetland size distributions. I compared projected lake and wetland sizes for 2010 with contemporaneous field measurements, and compared 1986 size projections with lake and wetland sizes derived from remote sensing and aerial photography.

4) Upscale projections for all three zones to estimate change in median lake and wetland size, AGB, and wetland plant diversity, as well as total surface area coverage and wetland AGB.

5) Project future change in lake and wetland size, plant biodiversity and wetland AGB, in all zones, under the assumption that the statistical relationships derived in objective 1 will remain unchanged until 2100. In this analysis, I used the three zones described in objective 2 to represent hypothetical future scenarios to assess the potential long-term effects of continued lake shrinkage and inter-annual variability in lake size.

6) Assess the vulnerability of lake sediment C to decomposition after exposure to aerobic conditions, and project future change in lake and wetland below-ground C. These projections were a first-order attempt to address the potential for reductions in below-ground C storage associated with widespread boreal lake shrinkage, because I was only able to sample lake sediment C at two lakes and had to rely on lake size-C stock relationships from the literature instead of fitting my own statistical models. Below-ground C projections are included in an Appendix at the end of the chapter.

I evaluate the plausibility of model projections by comparing them with previous literature and with the results of chapters 2 and 3. I then conclude by discussing the collective implications of these projections for the management of biodiversity, wildlife habitat, and C storage on National Wildlife Refuge lands characterized by shrinking lakes.

Methods

Study site description

The study area was located in the lowlands of the Yukon River floodplain, within the boundaries of the YFNWR, Alaska (Fig. 4.1). The YFNWR contains over 40,000 small lakes ranging from <1 ha to over 1000 ha in size, interspersed within a complex arrangement of wetland and forested habitat (Gallant 1998). This diverse landscape is ecologically significant and economically valuable as habitat for wildlife, including black bears and moose, and supports high breeding densities of waterfowl and other migratory birds (USFWS 1987). Like most Alaskan wildlife refuges, YFNWR also contains small villages (population < 1000). The residents of these villages are subsistence-based, depending on local wildlife populations and water resources (Riordan et al. 2006). Within the study area, approximately 10% of lakes have

shrunk significantly in the last 30 years, while an additional 25% appeared smaller in 2009 than in 1979, but did not follow statistically significant shrinking trends because of high intra- and inter-annual variability in lake size (Rover et al. 2012).

I identified all floatplane-landable lakes within the study area, which were defined as lakes at least 1 km long on one axis, using the National Hydrography dataset (nhd.usgs.gov). I then selected 48 Focal sites using a Generalized Random Tessellation Stratified design, which provided a spatially balanced random sample that was statistically representative of the study area as a whole. Field crews visited all lakes within 1 km of a focal site, yielding a total of 130 lakes (Fig. 4.1). Plant community characteristics were measured at each of these 130 lakes (referred to as 'field-sampled lakes' throughout this chapter).

Wetland community types

Lake-margin plant communities in the Yukon Flats follow a repeating sequence associated with declining soil moisture moving away from the water's edge (see Chapter 2). This sequence progresses from herbaceous nearshore communities dominated by grasses and sedges (GS), to a deciduous shrub band (SH) composed mainly of *Salix* spp, with occasional *Alnus* and dwarf *Populus* tree spp., followed by upland forest composed of a mosaic of Alaskan birch (*Betula neoalaskana*), Aspen (*Populus balsamifera*) and spruce trees (*Picea glauca* and *Picea mariana*). Overall, the Yukon Flats is an arid environment receiving little rainfall, and upland forest communities are characterized by dry soil and thin organic layers (Gallant et al., 1998). Plant growth, succession and C cycling in upland boreal forest communities are sensitive to climate feedbacks related to temperature, permafrost degradation, and wildfire occurrence (Mack et al. 2008, Jonsson and Wardle 2010, Johnstone et al. 2010, Goulden et al. 2011, Jorgenson et al. 2013). In this study I focused on the GS and SH communities, which showed clear

associations with the distribution of lakes (Whitehouse and Bayley 2005), and which provide unique habitat and forage types for local wildlife (Roach and Griffith 2015).

Vegetation surveys

Vegetation surveys were conducted from 2010 to 2012, as part of the Yukon River Basin project, a larger effort to understand the effects of climate change and disturbance on the Yukon River Basin (YRB) in Alaska (see Halm and Griffith 2014; Roach and Griffith 2015; https://alaska.usgs.gov/science/program.php?pid=36). Four 100m vegetation transects were established at each of the 130 field-sampled lakes. Transects were located using a random start azimuth, and ran perpendicular to the water's edge. Each transect was subdivided into three plant community types (GS, SH, and Forest), if present, based on visual estimates of when each of these three growth forms exceeded 50% of canopy coverage. The length of each plant community was measured along all transects. These lengths were averaged and used to create GIS layers representing concentric bands of GS and SH habitat around each lake. These GIS layers were then used to estimate GS and SH habitat area. All GIS analyses were conducted in R, using the rgeos and rgdal packages (Bivand et al. 2011, Pebesma et al. 2012). As described in Chapter 2, field crews also recorded all vascular plant species found along each transect. These surveys were integrated with plant functional trait data from an online database (www.try-db.org) (Kattge et al. 2011) and were used to estimate a community-specific index of plant functional divergence called Rao's quadratic entropy, which is referred to as functional divergence throughout this dissertation (Rao 1982). As described in Chapter 2, Rao's quadratic entropy is a measure of the total multivariate distance in functional trait values between species pairs, with each pairwise comparison weighted by the relative abundance of the two species. Rao's quadratic entropy is maximized when a community contains a wide range of trait values

that are evenly distributed among species. Functional divergence was calculated using a set of five effect traits related to rates of C and biomass accumulation and decomposition, and five response traits relevant for understanding community responses to lake change and disturbance (Chapter 2).

Vegetation: Above-ground biomass

Field biomass measurements were collected at 14 lakes (6 stable lakes, 4 shrinking, and 4 variable/flooding lakes). Understory biomass (g/m^2) for each plant functional type was estimated with destructive quadrat harvests (Fahey and Knapp 2007) collected in a two-week period corresponding to peak biomass (late July-early August). Ten 20x50cm quadrats were distributed randomly along a 60 m perpendicular sub-transect in each plant community type (GS, SH, and Forest). All sub-transects were centered on one randomly selected 100m vegetation transect, and located at the midpoint of each plant community type along that 100m transect. Samples were kept cool and were frozen within 1-2 days of collection. Thawed samples were dried at 60^{o} C for 48 hours, sorted by functional types, and weighed to estimate total biomass (Shaver and Chapin 1991). I estimated C content by multiplying biomass by 0.46, based on the average C content of above-ground tissue samples from representative vegetation types in the study area (Appendix C).

Overstory (tree and shrub) biomass was estimated using measurements of stem density, stem diameter, and species-specific allometric equations (Bond-Lamberty et al. 2002, Yarie and Kane 2007, Berner et al. 2015). Tree and shrub stem densities were estimated for each plant community type using variable-area transects (Engeman et al. 1994). Field crews randomly selected one 100m transect at each lake, then located perpendicular 60m density transects centered on that transect, at the midpoint of each plant community type. The 60m transects were

subdivided into six 2m wide search areas. Each area was searched until the first 5 tree and shrub stems were detected. The distance from the starting point to a point parallel to the fifth individual was used to measure the final segment length, and to calculate stem density (5 stems / 2*segment length in m). If <5 stems were detected after reaching the end of the 10m-long search area, stem density was calculated as the number of stems divided by 20 m^2. Diameter at breast height measurements were taken for all trees, and basal diameter for all trees and shrub stems < 10m tall. These measurements were used to generate allometric biomass estimates, which were multiplied by stem density to yield estimated biomass per m^2. These areal estimates were then averaged over the six segments in each plant community type. This method is a robust means of estimating stem density in variable environments while maintaining a constant sampling effort (Engeman et al. 1994).

Because allometric models of shrub biomass are site specific (Berner et al. 2015), field crews measured shrub stem biomass directly by harvesting 10 shrub ramets at each lake, stratified proportionately to the density of stems across community types. Ramets were dried and weighed following the same methods as those used for understory harvests. I multiplied mean ramet AGB by mean stem density to generate an estimate of total shrub biomass per m^2.

As described in Chapter 2, I used field estimates of total AGB (the sum of understory, shrub, and tree biomass) to validate a published GIS map of AGB covering the entire study area (Ji et al. 2012). I then used the published map to estimate mean AGB in Mg/ha for each wetland community type (GS and SH) at all 130 field-sampled lakes as well as the surrounding upland forest (F) community, although I focused only on wetland AGB in this study.

Soil C

To characterize the physical environment in each wetland plant community, field crews measured soil horizon thickness, C content, and soil moisture. Crews collected three soil cores in each plant community type (9 total) at each of the 14 lakes where AGB was estimated. Cores were collected using a rotating soil core (20cm x 4.8 cm diameter) with a cutting edge attached to a power drill, to minimize compression of the organic layer during sampling. The depths of fibric and organic horizons were recorded in the field, and samples were kept cool and were frozen within 1-2 days. Cores were split in half vertically, and one half was dried, ground, and analyzed for C content using a LECO 1000 CHN analyzer in the UAF Forest Soils Laboratory. The other half of each core was dried at 105° C and weighed to estimate bulk density (Michaelson et al. 1996) and moisture content. C content, moisture, and bulk density were calculated separately for all layers, including mineral soil and limnic (lake sediment) layers when present.

To upscale SOC estimates to all 130 field-sampled lakes, I derived a linear relationship between organic horizon thickness and total C content at all lakes where soil cores were collected (Johnson et al. 2011). I then applied this relationship to predict SOC values for all communities at all lakes using measurements of organic horizon thickness. Details of this analysis are described in Chapter 2. Because I did not measure seasonal thaw depth simultaneously at all lakes, I used a published map to estimate active layer thickness for each community and sampling lake (Pastick et al. 2013). I did not directly sample below-ground biomass due to logistical constraints. However, I did measure fine-root production within a single growing season using in-growth screens at a single lake (Lake 1_99_1), which were 10x20cm pieces of mesh screen installed vertically in the soil at the beginning of the growing

season. Fine root production was assessed by measuring the abundance, diameter, and mass of fine roots found growing through the screens within a 10 x 10 x 20 cm surrounding block of soil at the end of the growing season.

Lake C Pools/Lake Sediment C chronosequence

Filtered and unfiltered 1 L water samples were collected at a depth of 0.5m at all lakes and kept cool until they could be removed from the field. DOC content was analyzed at the USGS NRP laboratories in Boulder, Colorado (Schuster 2001, Halm and Griffith 2014). Organic lake sediment C was not directly sampled, which constrained me from projecting landscape-scale change in total soil C associated with lake shrinkage. However, colleagues from the USGS also collected complete limnic sediment cores (down to the mineral horizon), from the basin of a single lake (lake 1_99_1) in 2010. At the time of sampling, lake 1_99_1 had shrunk by 99% compared to it's size in 1986. Three replicate cores were taken at each site, separated by soil horizon, dried at 65° C to estimate bulk density, and analyzed for % C content, to calculate total C storage (Equation 4.1)

(4.1) $$Total\ C = bulk\ density\ (dry\ g\ soil\ /\ cm^3) * \%\ C * core\ volume\ (cm^3)$$

I contrasted limnic C stocks from this lake with GS and SH limnic horizons at lake 1_99_1 and at an adjacent shrinking lake (lake 1_99_2), and compared C stocks with wetland age estimates based on GIS analysis of when sample transects were last inundated. Although insufficient to provide a reliable estimate of lake C stocks for the whole study area, these field measurements provided some indication of limnic sediment C lability and vulnerability to deomposition after drying. I also estimated lake sediment C stocks using a published regression equation relating organic lake sediment C to lake area from a large sample of Finnish boreal lakes (R^2=0.47, n=118) from comparable latitudes (Kortelainen et al. 2004). Although not included in this

chapter, I did use modeled lake C stock estimates to project net change in lake and wetland C storage over time (see Soil C projections section; Appendix B).

Fire History

For each lake type (stable, shrinking, and flooding), I estimated the probability of having burned in the last 50 years. I calculated this value by overlaying sample lake locations with a GIS map of historical fire perimeters from 1950 to the present (fire.ak.blm.gov) and dividing the fraction of lakes overlapping a recent fire perimeter with the total number of lakes of each type.

Lake trend estimation

I estimated lake size trends using the methods developed by Roach et al. (Roach et al. 2011; Roach et al. 2013). Lakes were classified using a time series of 22 Landsat satellite images collected between 1979 and 2011. These images were converted to shapefile lake maps in ArcMap 10.0 as part of a larger study on long-term lake trends in the YFNWR (Rover et al. 2012). I fit linear models using area measurements for each lake in each year where imagery could be obtained (Equation 4.2; Roach et al. 2011)

(4.2) $$Lake\ Area = \beta_1 * Year + \beta_2 * Day\ of\ year$$

The study area encompassed three zones (west, central, and east) that were used in previous analyses of lake size trends (Roach et al. 2013; Roach and Griffith 2015; Fig. 4.1). Between 1986 and 2009, the central zone was characterized by an average decline of 3% in lake area per year, while lakes in the west zone had an average increasing trend that was an order of magnitude smaller, 0.3% per year (Roach and Griffith 2015). Lakes in the east zone also had a positive average rate of change (0.32 % / year), but this trend was non-significant at $\alpha = 0.05$ due to high inter-annual variability in lake size (Roach et al. 2013; Roach and Griffith 2015). Spatial variation in lake area trends (estimated as the standard deviation of annual % change estimates

within a zone) was almost twice as large in the east zone compared to the west (West SD = 2.46, East SD = 5.06; Roach and Griffith 2015). The lake trend distributions in these zones can be thought of as representing three categories of lake trends (west = increasing, central = decreasing, east = fluctuating). A recent study of lake area trends in eight Alaskan National Wildlife Refuges found the three Yukon Flats zones represented the full range of trends observed throughout Alaska, and that lakes in the central zone have shrunk more rapidly, on average, than anywhere else in the state (Roach et al. 2013).

Wetland area models

Field measurements of wetland size and remote-sensing estimates of lake size were combined to fit statistical models of wetland presence/absence and area as functions of 2010 lake size and historical lake shrinkage rates. For each wetland type, I ran a logistic regression of the probability of occurrence as a function of lake area, lake area shrinkage rate, and interaction between the two. I also used a generalized linear model with Gaussian errors to predict wetland area as a function of the same set of predictor variables. Non-significant predictors were removed, beginning with interaction terms, until arriving at the most parsimonious model. These models represented two hypothesized mechanisms by which lake shrinkage could affect wetlands: 1) lake shrinkage created opportunities for wetland expansion through succession, in which case shrinkage rates would inversely correlate with wetland age and wetland area (Lowcock et al. 2012), and 2) GS and SH wetlands were distributed based on current environmental conditions, specifically a soil-moisture hydrosequence (see Table 4.1). Based on hypothesis two, I predicted that the area occupied by lake-margin wetlands could be predicted based on the current size of lakes (which should have been surrounded by a zone of elevated soil moisture). I fit these models with data from field-sampled lakes (n=130), but used model results

to project historical and future changes in wetland area based on expected changes in lake size for all lakes in the three study area zones (n=2565; see *Backcasting*).

Backcasting

I performed a Monte Carlo simulation to project change in lake size from 1986 to 2010 for all lakes in each of the three zones (n=2565 lakes; 699 in the western zone, 1129 in the central zone, and 737 in the eastern zone). The first step involved defining a normal distribution of projected lake sizes in 1986 and 2010 for each lake using the predicted value from the lake's regression model as the mean and the model RMSE as the standard deviation. I drew 100 lake sizes from these distributions for each lake at both time periods. I then projected 1986 and 2010 area for grass/sedge (GS) and deciduous shrub (SH) plant communities. For each of 100 projected lake sizes and lake shrinkage rates from the previous step, I drew 100 random projections of GS and SH occurrence and area from the probability distributions defined by my wetland area regression models, yielding a total of 10,000 projected habitat areas, This process was repeated for 1986 and 2010 with all lakes in each of the three zones.

After projecting habitat area, the final step was to project change in functional divergence (Rao) and AGB. This required fitting linear models to my field-sampled lakes dataset (n=130) with lake size, habitat area, habitat type, and habitat area*habitat type as predictors, then removing non-significant predictors until reaching the most parsimonious model. As with previous stages, normal distributions were defined for each variable with model predictions as the mean and model RMSE as the standard deviation, and 100 draws were made from each distribution for each of the 10,000 lake area - habitat area combinations, yielding 1,000,000 variable estimates for each lake in the three zones and each time period.

Projected lake and plant community sizes, as well as projected community characteristics were summarized by calculating the median of all projected values from all lakes within each zone, and across all three zones combined. I also summarized the variability in projected values using both the interquartile range (75th quartile - 25th quartile) in boxplots, and 95% confidence intervals around the median (CI) to contrast projected values between zones and time periods. Quantifying variability in projected wetland size allowed me to assess whether the size distribution of wetland patches became more homogenous over time, and to compare the magnitude of spatial variability in lake and wetland size at any time period with the magnitude of projected change over time. All analyses were conducted in R (R Development Team 2009).

Model Verification/Validation

To verify that projections accurately captured lake change dynamics between 1986 and 2010, and that they reproduced the spatial variability and associated uncertainty in 2010 landscape characteristics at individual lakes, I repeated the 2010-1986 lake and wetland area backcasting exercise for the 130 field-sampled lakes. I then compared the distribution of projected and observed sizes for each community type among all 130 field-sampled lakes in 2010. Because field data from 1986 were unavailable, I initially intended to validate backcasting projections by comparing model output with remotely sensed maps of vegetation change over time. However, previous studies have found that vegetation maps based only on Landsat-scale reflectance data have poor predictive power in lowland boreal regions when compared to field data (Lara et al. 2015). Instead, I used the National Wetlands Inventory map (https://www.fws.gov/wetlands/), which was derived from aerial photography collected between 1980 and 1985, as an independent comparison. The NWI map was the closest available match to the time frame of my historical projections, and included a set of simple cover types that closely

mirrored my plant community type classifications (Lakes/Ponds, Freshwater Emergent Wetlands, and Freshwater Shrub/Forested Wetlands). I identified lake polygons in the NWI dataset that overlapped the centroids of all 130 YRB study lakes, and extracted the area of those polygons as estimates of 1980's lake size. I also extracted the area of Freshwater Emergent Wetlands and Freshwater Shrub/Forested Wetlands within 100m of each NWI polygon representing one of my study lakes, to provide an estimate of lake-margin wetland area that would be comparable with estimates based on my field sampling design. I then compared NWI data with backcast estimates of lake, GS, and SH wetland size distributions in 1986. Finally, I also compared NWI and backcasting estimates of the total area occupied by my field-sampled lakes and associated lake-margin wetlands in 1986. NWI maps have not been validated against contemporaneously collected field data in my study area, or in other boreal lowland communities, so it is difficult to assess their accuracy or bias with respect to true cover types (Wilen and Bates 1995). However, the NWI has been shown to have high accuracy (80 %+) in mid-latitude temperate ecoregions (Wilen and Bates 1995), and provided a useful point comparison for assessing whether my projections of historical land cover produced realistic values.

Upscaling/lake change scenarios

In addition to projecting change in median lake/plant community size and diversity/AGB, I also calculated the total projected area occupied by lakes, GS, and SH, as well as the total GS and SH biomass, in each of the three zones (west, central, and east). Net AGB was estimated by multiplying projected density in C mass / m^2 by the total projected area of the relevant land cover type (e.g. GS AGB / m^2 * GS area). These totals were calculated for each zone, and for all zones combined. Finally, because the three zones were not equal in size, I multiplied all values by the

ratio: study area size / zone size. This allowed me to compare the landscape-level effects of projections among zones, and to assess the consequences of scenarios in which the entire study area experienced the distribution of lake trends representing each zone.

Future Projections

I conducted multi-stage Monte Carlo simulations for two future time periods (2010-2060 and 2060-2100) in all three zones to assess the potential long-term effects of the lake change scenarios that they represented (west=small, significant rate of increase, central=rapid decrease, east=high inter-annual variability with no significant trend). My methods were identical to those used for historical (backcasting) projections, except that projected rates of change in lake size for each projection interval were based on median projected lake sizes at the start of the interval (Roach and Griffith 2015). These rates were drawn by placing the median lake size at the start of the interval within one of five quantiles for each zone, and drawing from previously published normal distributions of lake trends for those quantiles within the three study zones (Figure 2 in Roach and Griffith 2015). I did not use the regression models for individual lakes in future projections because lake size and annual trends were not independent, such that the smallest lakes tended to grow over time while the largest lakes were more likely to shrink (Roach and Griffith 2015). As a result, extrapolating a fixed rate of change in lake size beyond the historical period would have resulted in some negative or nonsensical lake sizes (Roach and Griffith 2015). After projecting future lake sizes, I repeated all of the other steps from the backcasting projection exercise (habitat area estimation, area-weighted mean functional divergence scores (Rao) and AGB projections).

Below-ground C projections

In addition to projecting change in wetland structure and plant community characteristics, I was also interested in assessing the vulnerability of wetland C stocks. However, to project change in soil C stocks driven by succession and lake shrinkage, it was necessary to make several assumptions. First, in the absence of lake sediment C data from my study area, I assumed that an empirical relationship between lake sediment C density and lake size in Finnish boreal lakes could be used to estimate C stocks in Alaska. I also assumed that average soil C density in a wetland of a given type (GS / SH) and size was constant, regardless of the age of wetland communities. This assumption was likely violated due to the time lag that typically occurs between the establishment of a new successional stage and the development of associated soils, as well as the influence of previous vegetation type and disturbance history (Walker et al. 2010). In particular, I only had lake-basin cores from a single lake with which to contrast lake-basin and wetland limnic stocks. This made it difficult to test the assumption that large buried limnic soil horizons did not persist after the replacement of lakes with wetlands. The presence of deep, persistent wetland limnic layers would likely cause overestimation of C losses. Because of these limitations, I did not make soil C projections a primary focus of this analysis. However, I did generate projections of soil organic C, lake sediment organic C, and lake dissolved organic C (DOC), based on the above assumptions, as a heuristic exercise. These projections have been included in an appendix (Appendix B), and their output is used for hypothesis generation to guide future research. Given the size of extant wetland and lake C stores throughout the boreal region, there is a compelling need to provide a first-order picture of the potential range of C losses that could be associated with lake shrinkage and land cover change.

Results

Wetland area models

GS wetland area was significantly positively correlated with lake area, but not with lake shrinkage rates, while the probability of GS occurrence did not correlate with either predictor (Table 4.2). Lake size explained 22% of observed variation in GS wetland size (Table 4.2). For SH wetlands, the results were more complex. SH area was strongly positively correlated with lake area, but also positively correlated with lake shrinkage rate and a significant negative interaction term (Table 4.2). However, the correlation between SH size and lake shrinkage rate was weak, and lake area alone explained 29% of observed variation in SH area. The probability of shrub occurrence was not correlated with either lake size or lake shrinkage rates (Table 4.2).

Lake/Wetland size backcasting/Model verification

Projected estimates of surface area for field-sampled lakes in 2010 were nearly unbiased with respect to observed 2010 sizes on average: (ln(observed size) = 0.855*ln(projected size)+1.6428, R^2=0.66, $p < 0.0001$; Fig. 4.3A). There was no significant difference between median projected and observed GS and SH 2010 sizes among all field-sampled lakes (GS: t=0.23, df=137.41, p=0.82; SH: t=-0.93492, df=232.05, p=0.35; Fig. 4.3B). Median projected GS/SH size ratios were also similar to observed ratios among all field-sampled lakes. The mean across all lakes of median projected values was 0.93 (CI=0.92-0.94), while the mean of observed values was 0.966 (CI=0.91-1.02). Among all field-sampled lakes, median projected GS/SH size ratios were not significantly different from observed ratios (t=-1.0963, df=118.1, p=0.2752).

When YRB projections of 1986 lake and wetland size were compared with NWI-derived estimates, YRB projections consistently produced smaller estimates of lake and wetland size in 1986 compared to NWI data (Fig. 4.3C). Among all 130 field-sampled lakes, median lake size

from the YRB model was only 66% of mean NWI lake size (17,000 m^2 versus 26,000 m^2), while median GS size from the YRB model was only 37% of median NWI GS size (20,000 m^2 versus 53,000 m^2). Median SH size projections were within 2% of each other (median NWI SH size = 43,000 m^2; median YRB SH size = 42,000 m^2; Fig. 4.3C). Median GS size differed significantly between YRB and NWI projections, but median SH and lake sizes did not (Fig. 4.3C)

YRB estimates of total Lake, GS, and SH area were also consistently lower than estimates from the NWI. On average, total surface area estimates for 130 lakes from the YRB model were 69% of NWI estimates, across all three communities. The total surface area of field-sampled lakes in 1986 based on the YRB model was 88% of total NWI surface area for the same set of lakes (60.65 km^2 versus 53.67 km^2), while total YRB GS area for the same lakes (3 km^2) was 44% of the NWI estimate (6.8 km^2), and total YRB SH area (5.4 km^2) was 75% of the NWI estimate (7.3 km^2; Fig. 4.3D). Statistical differences between YRB and NWI total area estimates were not computed because no estimate of uncertainty was available for the NWI values.

Lake and wetland size projections

Median projected lake size among lakes in all zones combined decreased by 61% from 1986 to 2100, from 13425 m^2 (CI=12537-14326) to 5299 m^2 (CI=5045-5535) (Fig. 4.4A). I projected smaller declines in median GS (mean proportional decrease =0.43, CI=0.41-0.45; Fig. 4.4B) and SH wetland size (mean proportional decrease =0.37, CI=0.35-0.39; Fig. 4.4C). The median ratio of GS to SH wetland size per lake showed little variation between 1986 (mean=0.42, CI=0.41-0.43) and 2100 (mean=0.38, CI=0.38-0.38) in all zones combined, but overall the ratio of lake size to the size of adjacent wetlands (GS area + SH area) decreased from 0.53 (CI=0.51-0.55) to 0.34 (CI=0.33-0.35). In the west zone, median lake, GS, and SH size all increased slightly between 1986 and 2010 because many lakes were in the smallest quantile of

1986 lake sizes, and were projected to grow rapidly in the 1986-2010 interval (see Roach and Griffith 2015). Median lake and wetland size in the west zone declined slightly beginning in 2010, because lakes in all but the smallest initial size quantile had negative annual size trends. In contrast, median lake and wetland size decreased consistently over time in the eastern (high variability in lake size) zone, with net declines of ~36% for all three cover types between 1986 and 2100 (e.g. GS 1986 = 7770 m^2, CI=7298-8408; 2100 = 5005.10, CI =4697-5277). In the central zone, where lakes decreased in size three times faster than the average trend for all zones combined, median lake size was projected to decrease by more than 80% from 1986 to 2100 (1986 =12683 m^2, CI=11392 -13551; 2100 mean=2473, CI=2277-2588; Fig. 4.4A). Median GS and SH wetland sizes in the central zone were projected to decrease by 57% (CI=54-60%) and 49% (CI=46-52%), respectively, over the same time period (Fig. 4.4B, Fig. 4.4C). These trends resulted in a substantial drop in the median lake size:wetland size ratio (1986 = 0.52, CI=0.48-0.56; 2100 = 0.20, CI=0.19-0.21) and an increase over time in the median ratio of SH to GS wetland size (1986 = 2.39, CI=2.30-2.48; 2100 = 2.86, CI=2.83-2.89).

On average, the proportion of total land surface occupied by lakes, GS, and SH declined by 29%, 36%, and 35% respectively, although overlap between 1986 mean lake coverage and 2100 confidence intervals suggested that the loss of total lake area was not significant. Across all zones combined, the fractional coverage of lakes dropped from 5.60% of all land surface area (CI=4.1-6.4) in 1986 to 4.00% (CI=3.80-5.80) in 2100, while over the same period, GS coverage went from 0.80% (CI=0.78-0.83) to 0.51% (CI=0.48-0.53) and SH went from 1.70 % (CI=1.60-1.70) to 1.10 % (CI=1.10-1.20). The high rate of lake shrinkage in the central zone led the fractional cover of lakes on the landscape to decrease by an order of magnitude (1986 mean = 6.40%, CI= 3.70-4.90; 2100: mean=0.32 %, CI= 0.41-0.70; Fig. 4.5A), in contrast to smaller

proportional decreases in the fractional coverage of GS (1986 mean = 0.80%, CI=0.78-0.83; 2100 mean= 0.51%, CI=0.48-0.53; Fig. 4.5B) or SH (1986 mean = 1.70 % CI = 0.017-0.017; 2100 mean = 1.10%, CI= 1.10-1.20; Fig. 4.5C). The net result was that the ratio of wetlands to lakes in the central zone was projected to increase from 0.50 in 1986 (CI=0.44-0.56) to 3.84 in 2100 (CI=3.60-4.08). In the west (increasing lake size) zone, total lake surface area and total GS and SH cover were stable (within 10% of 1986 values) throughout the projection period (Fig. 4.5). In contrast, total lake surface area increased between 1986 and 2100 in the eastern (fluctuating lake size) zone (mean proportional increase =18%, CI=16-20; Fig. 4.5A), while the total area of GS and SH decreased by 22% (CI=20-24) and 21% (CI=18-23) respectively (Fig. 4.5B and Fig. 4.5 C).

Functional diversity projections

When functional divergence (Rao) was predicted using data from field-sampled lakes, the top model included lake size and wetland area in both GS and SH communities (Table 4.3). Lake and wetland size explained substantially more variation in GS Rao than in SH Rao ($R^2 = 0.33$, $p<0.0001$ for GS Rao model; $R^2 = 0.08$, $p=0.05$ for SH Rao; Table 4.3). GS Rao was negatively related to both lake size and GS wetland size, whereas SH Rao was negatively related to SH wetland size, but positively correlated with lake size (Table 4.3). GS Rao values increased threefold in GS wetlands (Fig. 4.6 A) from 1986 (mean=10.21, CI=10.08-10.35) to 2100 (mean=32.74, CI=31.94-33.63). In contrast, mean SH Rao values only increased by 50% (Fig. 4.6B) from 1986 (mean=11.56, CI=11.46-11.66) to 2100 (mean=18.51, CI=18.29-18.74). The discrepancy in median projected Rao values between GS and SH was most pronounced in the central zone, where lake and wetland size decreased most rapidly. The area weighted average GS Rao value in the central zone increased by 600 percent from 1986 (mean=10.22, CI=10.04-

10.41) to 2100 (mean=61.41, CI=61.17-62.63), while average central SH Rao scores increased by only 30% over the same period (1986 mean=11.38, CI=; 11.22-11.52; 2100 mean=15.04, CI=14.98-15.10), a smaller increase than was observed in the other two zones (Fig. 4.6). Projected Rao values in both plant communities were similar between the eastern and western zones, despite the eastern zone having almost twice as much inter-annual variability in lake size (Fig. 4.6).

AGB projections

For GS and SH communities, the combination of lake size and wetland size explained 10-15% of observed variation in AGB density (g/m^2) among field-sampled lakes (Table 4.3). AGB density (kg/m^2) was positively correlated with lake size but negatively correlated with wetland size in both communities (Table 4.3). Total projected wetland AGB stocks for all zones combined increased by 30.8% between 1986 (mean= 0.48 Tg, CI= 0.46-0.49) and 2100 (mean= 0.63 Tg, CI= 0.60-0.65; Fig. 4.7). Total western zone AGB was projected to increase by 87.7% (1986 mean =0.53 Tg, CI=0.50-0.56; 2100 mean = 0.99 Tg, CI=0.94-1.04) and eastern total AGB was projected to increase by 58.25% (1986 mean Tg = 0.13, CI=0.12-0.14; 2100 mean: 0.22, CI = 0.21-0.24; Fig. 4.7). In contrast, the total central zone wetland AGB was projected to decrease by 27.5% (1986 mean = 0.63 Tg, CI=.60-0.66; 2100 mean = 0.45, CI=0.45-0.46) despite projected increases in AGB density per m^2, due to projected declines in total GS area between 1986 and 2100 within that zone (Fig. 4.7A). In the eastern zone, total wetland AGB increased significantly, from 0.34 Tg (CI= 0.312-0.36) in 1986 to 0.536 (CI=0.50-0.57) in 2100. The ratio of total GS AGB stock to total SH AGB stock was relatively constant and close to 2:3 for most zones and for all zones combine (mean for all zones and years=0.63, CI=0.58-0.68), but

the ratio shifted towards SH dominance in the central scenario, nearly reaching a 1:2 ratio by 2100 (mean=0.53, CI=0.53-0.53).

Lake sediment C

Lake 1_99_1 shrunk by almost 90% between 1986 and 2010 (Fig 4.8C). The rate of shrinkage was approximately linear over 30 years, but with three distinct stages during which lake size was stable for 5-10 years (Fig. 4.8C). GIS analysis indicated that the vegetation and soil transects established for measuring GS and SH characteristics at this site occupied ground that was covered by the lake until between 2005 and 2007 (Average age = 4 years in 2010). The other lake at this site (1_99_2) had also shrunk significantly over the last 30 years (Fig. 4.8D), but the position of the lakeshore at the vegetation sampling transect was relatively stable over time, and transect location would have been exposed between 1986 and 1994 (Average age = 20 years in 2010). Soil transects at these two lakes were ~800 m apart in 2010, and the two lakes were less than 400 m apart at their maximum measured extent in 1986. GS and SH wetlands were similar in species composition between the two lakes (V. Patil, unpublished data).

At lake 1_99_1, limnic C stocks per m^2 in GS and SH wetlands were 77% and 59% of C stock densities in lake sediments, respectively, and the GS and SH limnic horizon were 35% and 42% thinner, respectively, than the lake basin limnic horizon (Fig. 4.8A). The contrast with lake sediment C from Lake 1_99_1 was even more dramatic at wetlands in Lake 1_99_2, which had been established an average of 20 years ago (Fig. 4.8B). At these older wetland sites, limnic soil was only detected in one of three replicate GS soil samples, and was completely absent from SH samples. Similarly, mesic horizons were only observed in 4 cores, from three lakes, among all lakes with soil data. The average thickness of the mesic horizon, where present, was 3 cm. On average, GS limnic stocks were roughly 98% lower at Lake 1_99_2 than at Lake 1_99_1. Mean

measured lake 1_99_1 limnic soil C (61 kg / m^2) was higher than the modeled estimate based on 2010 lake size and equations in Kortelainen et al. 2004 (47.33 kg / m^2), but the modeled estimate was within 1 SE of the average measured value (Fig. 4.8A).

Discussion

Overview

Overall, results supported my hypothesis that boreal lake size is a substantial influence on wetland size and wetland characteristics related to biodiversity, wildlife habitat, and C storage, and that continued reductions in lake size may have landscape-scale effects. Linear models demonstrated significant positive correlations between lake size and wetland size, and negative correlations between wetland size and wetland characteristics (Rao and AGB). Projections based on these results indicated that sustained future reductions in lake size will decrease total wetland surface area and increase the relative abundance of woody versus herbaceous wetland plant communities. The projected increase in woodiness was associated with projected increases in AGB and plant functional divergence (Rao) at the landscape scale, except in the central zone where total lake surface area, total wetland surface area, and the total wetland AGB stock were all projected to drop sharply. Total and median lake surface area were projected to increase slightly in the eastern zone compared to the western zone, due to the effect of high inter-annual variation in the east zone on the range of projected lake sizes. However, these difference were small, and were not associated with differences in wetland size or the relative abundance of SH or GS wetlands. Overall, my findings reinforce previous research demonstrating the importance of land-cover change via succession and disturbance as a driver of ecosystem function (Chapin et al. 2005, Euskirchen et al. 2009, Jorgenson et al. 2013, Pastick et al. 2014).

Projected effects of rapid lake shrinkage

The YFNWR is a useful case study for examining the regional effects of lake shrinkage because it contains sub-regions representing the full spectrum of long-term lake surface area dynamics that have been observed throughout Alaska, with the central zone representing the most rapid lake shrinkage rates in the state (Roach et al. 2013). In terms of land cover and habitat change, lake shrinkage increased the relative size & abundance of woody (SH) versus herbaceous (GS) wetlands, but only in the central zone where lake shrinkage was most rapid (Fig. 4.3). In addition, central zone functional trait divergence (Rao) increased more over time in GS communities compared to SH (Fig. 4.6). Rao scores were positively associated with the relative abundance of traits associated with woody shrubs, which is consistent with the interpretation that rapid lake shrinkage promotes the encroachment of woody vegetation into the edges of GS wetlands (see Chapter 2). Although my methods were not well suited to identifying the mechanisms responsible for these changes, increased 'shrubiness' can result from a positive feedback between decreased soil moisture and the growth of deciduous shrubs, which transpire water significantly faster than herbaceous fen vegetation (Klein et al. 2005, Talbot et al. 2010). My projections, which were based on correlations between current lake size and GS/SH wetland size in my study area, are consistent with recent evidence of a link between lake drying and shrub encroachment on the Kenai Peninsula (Klein et al. 2005).

AGB regression models fit to field sampling data were generally consistent with the results for functional diversity (Rao), in that GS and SH AGB density (kg/m^2) were negatively correlated with wetland area (Table 4.3). These results implied that AGB was influenced by edge effects, including the encroachment of woody vegetation into herbaceous (GS) communities and of tree species into the deciduous shrub community (Chapter 2). Inverse relationships between

AGB density and wetland size buffered total regional AGB stocks against the effects of lake shrinkage, such that GS and SH AGB increased over time in projections for all zones combined. However, GS and SH AGB stocks did decline over time in the central zone, where the loss of lake and wetland area was most pronounced.

Projected effects of lake size variability

Overall, the projected effects of high inter-annual variability in lake trends on lake and wetland properties were ambiguous. The effects of high inter-annual variability should have been evident in contrasts between projections from the east zone and the west zone. The eastern zone represented a scenario in which lake size was approximately twice as variable from year to year as in the western zone, although the two zones had similar long-term trends in mean lake size. In a study of historical lake trends throughout the state, the eastern zone ranked first out of 8 study areas in terms of variability associated with long-term lake size trends (Standard errors from regression models of lake size vs. time; Roach et al. 2013). I contrasted projections from the eastern zone with those of the western zone because inter-annual fluctuations in lake size and water level can have important ecological effects, including increased plant diversity, altered community composition, high mortality of woody vegetation, and reduced organic C storage (Asada et al. 2005; Wantzen et al. 2008). Because greater inter-annual variability meant that the distribution of east zone lake sizes had longer tails, and because small lakes tended to grow over time while large lakes were more likely to shrink, on average the east zone lake size distribution became increasingly right-skewed. As a result, a few lakes were projected to become several orders of magnitude larger than average, and total lake surface area increased over time despite a significant decline in average lake size, as opposed to the western zone where total lake area appeared to decline over time. However, neither the increase in total east zone lake area between

1986 and 2100 nor the decrease in total west zone lake area were significant based on 95% confidence intervals. Nevertheless, my results illustrate how high variability in lake size trends can produce a few very large lakes with disproportionate influence on the total surface area of lakes. Variability in lake trends had a weaker projected effect on total GS and SH wetland area, both of which had non-significant decreasing trends between 1986 and 2100 in the east and west zones. This discrepancy between total lake area and total wetland area appears to be a function of the log-log relationship between lake and wetland size, meaning that change in the size of very large lakes had a proportionately smaller effect on adjacent wetlands than size changes at the smallest lakes.

Projections from the east zone are inconsistent with previous research, which has shown that lake size fluctuations are associated with disproportionately high mortality of woody vegetation and increased plant functional diversity in lake-margin wetlands (Asada et al. 2005). In fact, the average projected area ratio of GS/SH wetlands in the east zone increased significantly between 1986 and 2100 (Fig. 4.3), and although SH Rao scores increased significantly over time, SH Rao in the western zone increased by a similar amount (Fig. 4.6). There was less total AGB in the east zone at the end of the projection period, compared to the west zone, but this result was associated with the projected decrease in east zone total wetland area, rather than with a shift from woody to herbaceous vegetation. It is possible that eastern zone projections would be more realistic had I used field data to regress wetland diversity and composition based on historical variance in lake size, rather than the current lake size, and generated future projections accordingly. In the current model, I have greater confidence in my ability to project the ecological effects of a long-term lake shrinkage trend than in my ability to simulate the ecological effects of variability associated with that trend.

Mechanisms of projected change

My projections are based on a relatively simple set of linear models that link the size of lake and wetland ecosystems to each other and to the characteristics of those ecosystems. Although these models rely on statistical, rather than mechanistic, associations between lakes and wetlands, their results are plausibly consistent with independently derived estimates of past and present lake and wetland sizes. One possible exception is the negative bias in projected 1986 GS wetland sizes relative to NWI-derived estimates. As already noted, these differences are difficult to interpret because the NWI was not itself validated against contemporary field data from this ecoregion. However, at least part of this difference could stem from my definition of GS wetlands, which excluded any floating sedge-dominated vegetation mats that extended over the margins of lakes. These floating mats are common in the Yukon Flats, and are difficult to separate from terrestrial vegetation based on remote sensing (Roach et al. 2011), and could have been classified as freshwater emergent wetlands in the NWI dataset, driving up size estimates for that cover class.

Model projections are also consistent with previous work demonstrating the strong influence of land-cover on organic matter production, breakdown, and export from terrestrial sources into lakes (Gergel et al. 1999; Kortelainen et al. 2004; Jorgenson et al. 2013). The close relationship between lake and wetland sizes is not surprising given that boreal wetland plant communities tend to distribute along a moisture gradient (Sulman 2012; Talbot et al. 2010; Table 4.1). Wetland soil moisture is also related to lake dynamics, and is lower than average at shrinking lakes (Table 4.1). These relationships suggest that soil moisture provides a mechanistic explanation for why wetland communities shrink and expand through succession to track rapid changes in lake area, and why wetland and lake area were positively correlated. My projections

of functional diversity and AGB based on wetland area in zones with shrinking vs. increasing lake trends could be explained by a second important biological mechanism: edge effects in which woody vegetation can encroach on small patches of herbaceous wetlands (Chapter 2). Overall, the comparison of my results with previous research suggests that space-for-time models can provide useful insights into the role of lake shrinkage-driven succession as a driver of regional responses to climate change.

A key advantage of my approach to projecting landscape change is that it can be implemented using publicly available remote-sensing data. The same framework could therefore easily be extended to other locations, or be used to examine the effects of lake shrinkage on other important landscape characteristics such as seasonal thaw depth, which is tied to soil organic content, soil moisture, and vegetative cover (Table 4.1) (Jorgenson et al. 2013; Pastick et al. 2013). My results could also serve as a useful point of comparison for the projections derived from mechanistic simulation models, which are not ideally suited to representing landscape-scale successional change and fine-scale heterogeneity in vegetation cover (Hibbard et al. 2003, Wullschleger et al. 2014) and which will need to be validated by comparison against multiple lines of evidence, including space-for-time models (Rastetter 1996). However, it must be emphasized that these models were designed only to project the effects of shrinking lakes on plant communities in their immediate surroundings. In areas with few lakes, most land cover change could probably be attributed to other landscape processes such as wildfire, necessitating a different modeling approach.

Although my models omitted wildfire and other important landscape processes that could influence lakes and wetlands, spatial variation due to such processes is incorporated into my projections, due to the spatially representative field sampling design. Incorporating spatial

variation in fire history into data collection and modeling was critical, because wildfire is an important driver of succession and C cycling in boreal landscapes (Harden et al. 2000; Balshi et al. 2007; Yuan et al. 2012), and because recent fire history is associated with the probability of shrinking in previous studies of boreal Alaskan lakes (Roach et al. 2013). However, the effect of fire history on lake shrinkage was small relative to other landscape factors including soil type and proximity to rivers (Roach et al. 2013). In addition, fire history was not a significant predictor of lake area trends in my field-sampled lakes, possibly because proximity to rivers and other exogenous drivers were more important (Chapter 2). At field-sampled lakes, fire history was also not a significant predictor of GS wetland size, which may be buffered against burning by high soil moisture and the lack of woody fuels (Chapter 2). Finally, YFNWR lake ecosystems are also resilient to fire in terms of water chemistry (nutrients and C) and food web dynamics over timescales ranging from years to decades (Chapter 3) (Lewis et al. 2014), which may be related to the buffering effect of GS wetlands. In summary, although fire is an important disturbance agent in the region, lake area change is an important yet poorly understood disturbance agent in its own right, and apparent responses to lake shrinkage that were documented (shrinking lake-margin wetlands, increased wetland functional diversity and above-ground biomass) were unlikely to have been driven by fire history.

Implications: land cover

In sub-arctic Alaska, lake area trends and lake size are related such that on a long-enough time scale, lake size dynamics (and by extension, lake-margin wetland size) should be cyclic, similar to the long-term thaw lake cycles that have been documented in arctic Alaska (Roach and Griffith 2015). However, based on my projections, accelerated warming/lake shrinkage (e.g. central zone trends becoming widespread/normal) could perturb this equilibrium, with total lake

area shrinking by ~80% within a century in the central zone. Although extreme relative to current average lake trends across boreal Alaska, the scenarios represented by the central and eastern zones are likely to become increasingly widespread with continued warming, which is expected to influence both lake shrinkage rates and variability through its effects on fire, permafrost/soil drainage, water balance, and spring melt (Roach et al. 2011; Roach et al. 2013; Chen et al. 2012).

Implications: land management

Long-term loss of lake area has been documented throughout the boreal ecoregion, particularly in Alaska (Riordan et al. 2006). These trends are a potential management challenge on Alaska's National Wildlife Refuges, 11 of which occupy a combined 19.5 million hectares of boreal habitat dominated by lakes and wetlands (USFWS 2015). These refuges represent critical breeding habitat for dozens of waterfowl species as well as habitat for moose (*Alces alces*), black and grizzly bears (*Ursus americanus* and *Ursus arctos*), wolves (*Canis lupus*), marten (*Martes martes*), and other valuable wildlife species (USFWS 1987). In a recent study of eight boreal Alaskan National Wildlife Refuges including the Yukon Flats, four of the other seven refuges had statistically significant negative annual trends in lake area over the last 30 years (Roach et al. 2013), but the western and central Yukon Flats sub regions had the largest positive and negative trends, respectively, observed anywhere in the state (Roach et al. 2013). Within the Yukon Flats, current lake trends are projected to cause significant declines in local waterfowl species richness, and species that are already rare appear the most vulnerable (Roach and Griffith 2015). My results add to that story by illustrating how continued lake shrinkage could reduce both the total area occupied by wetlands and the variability of wetland patch sizes, while increasing the overall woodiness of lake-margin wetland plant communities. These changes would reduce the

availability of nesting habitat for local waterfowl, while at the same time local increases in woody shrub biomass could be beneficial for moose (Seaton et al. 2011). In addition, lake shrinkage may reduce the size of boreal lowland organic C stocks, which could be considered components of the 'biological integrity, diversity and health' of wildlife refuges like the Yukon Flats (Meretsky et al. 2006). There is growing recognition that C storage represents an additional wetland ecosystem service provided by National Wildlife Refuges, and should be conserved (Ingraham and Foster 2008; Patton et al. 2015). My projections could be used to help refuge managers assess how continued warming and lake shrinkage might affect the overall value of refuge lands, and to develop appropriate responses.

Implications: Climate C feedbacks

Given the widespread evidence for shrinkage of boreal lakes and wetlands, associated loss of organic C stocks could represent an important high-latitude climate feedback. Globally, the total C stock represented by boreal lake sediments has been estimated to range between 20 and 120 Pg (Molot and Dillon 1996; Kortelainen et al. 2004). This range represents only a small fraction of the estimated 1035 Pg C stored in near-surface (<3m) boreal and arctic soils (Schuur et al. 2015). However, estimates of boreal lake stocks are similar to the range of modeled cumulative C emissions from thawing permafrost over the next 100 years (mean = 92 Pg, range = 37-174 Pg; Schuur et al. 2015). In other words, the release of all boreal lake and wetland C into the atmosphere by 2100 could roughly double projected emissions from the permafrost zone. Although this scenario is unlikely, my land cover change projections indicated that areas like the Yukon Flats could experience anywhere from a 10% increase in lake and lake-margin wetland C stocks to an 86% decrease over the next century, depending on long-term trends and short-term variability in lake size (Appendix B). Those projections required the assumptions that limnic

sediment C is rapidly metabolized after drying, and that sediment C density and lake size co-vary similarly in Alaskan and European lakes. However, my field data, albeit limited, suggested that both of these assumptions were reasonable (Fig. 4.8), and lake-size-C storage relationships similar to the model I used have been described in boreal landscapes around the world (Ferland et al. 2012). If rapid lake shrinkage similar to YFNWR central-zone trends occurred throughout the boreal region, it would represent a significant increase in high-latitude C emissions associated with warming and permafrost thaw. Unfortunately, boreal lake shrinkage trends are not well documented outside of a few regions of Alaska. A circumboreal monitoring effort and expanded field sampling of boreal lake C stocks and lake area dynamics could significantly improve our understanding of permafrost region climate feedbacks.

Summary/Conclusions

Lake area change is an important driver of vegetative succession in the boreal lowlands of the Yukon Flats, and is expected to cause landscape-level changes in plant biodiversity, wildlife forage availability and habitat quality, and organic C storage over the next 100 years. The magnitude of these changes are sensitive to both the rate of lake shrinkage and annual variability in lake size, both of which are likely to increase based on projected future warming trends. In particular, rapid lake shrinkage is likely to reduce the availability of wetland breeding habitat for migratory waterfowl, while the remaining wetlands will probably become increasingly shrubby, increasing their habitat value for moose and other browsers. My space-for-time model provides a relatively simple framework for assessing the magnitude and spatial variability of these changes in habitat availability and C stocks. The quantitative projections described here could be useful as points of reference for simulations from more sophisticated process-based models and could also help land managers make informed decisions about the

present and future value of Alaska's boreal wetland complexes. Finally, although there is still significant uncertainty around estimates of boreal lake and wetland C stocks, boreal lake shrinkage has the potential to significantly increase boreal C emissions over the next century, and the magnitude of this increase could be comparable to projected emissions associated with permafrost thaw.

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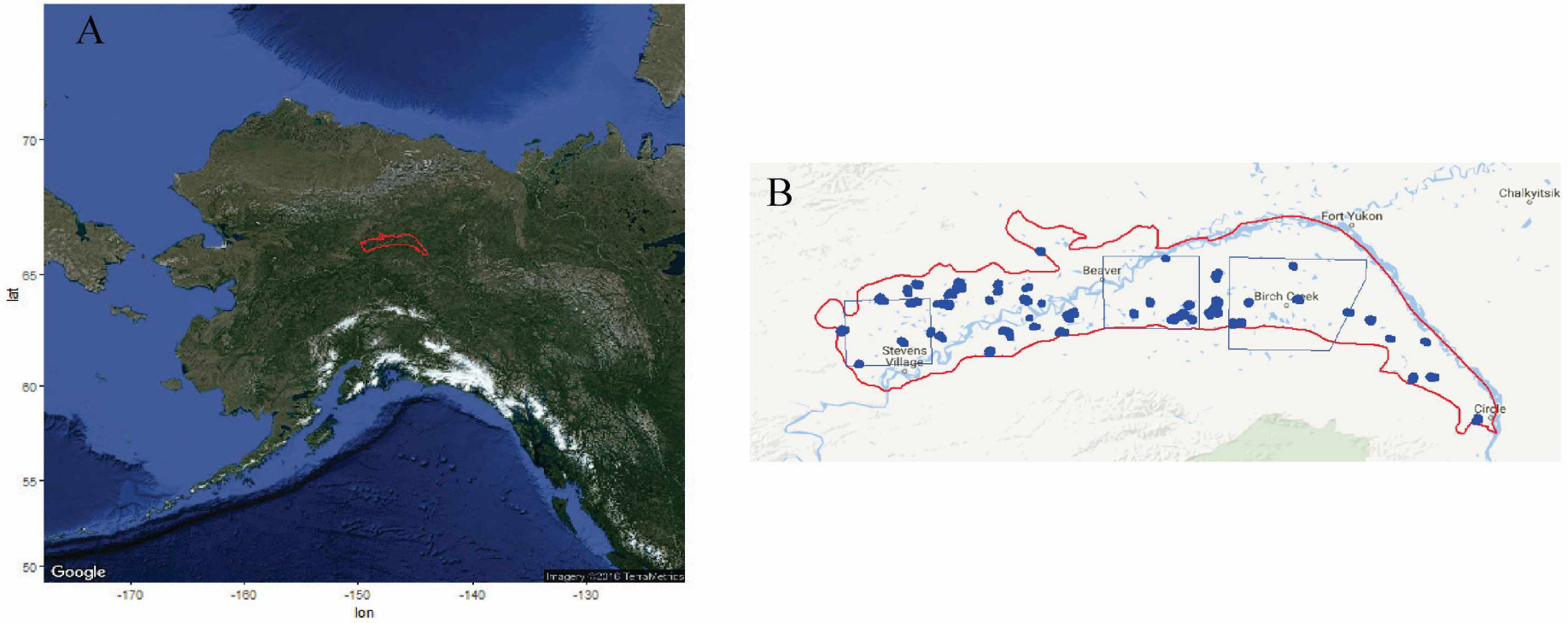

Figure 4.1. Study area map. Overview map (panel A) and close-up map of study area (panel B). This study used data on lake and wetland characteristics from a sample of 130 field-sampled lakes (blue circles, panel B) representing a spatially balanced random sample of lakes throughout the lowland floodplain of the Yukon Flats National Wildlife Refuge in northern Alaska (3.5 million hectares; red polygon, both panels). Relationships between lake size, wetland area, and lake/wetland characteristics (carbon stocks and plant functional diversity) were applied to all 2565 lakes in three zones (blue polygons), representing three distinct combinations of long-term trends and inter-annual variation in lake surface area (Roach and Griffith 2015, Roach et al. 2011). The west zone was characterized by a small significant increasing trend in lake area and low inter-annual variation, the central by a significant decreasing trend and low variation, and the east by a small, non-significant increasing trend and high inter-annual variation. Map data: Google, Landsat/Copernicus, IBCAO.

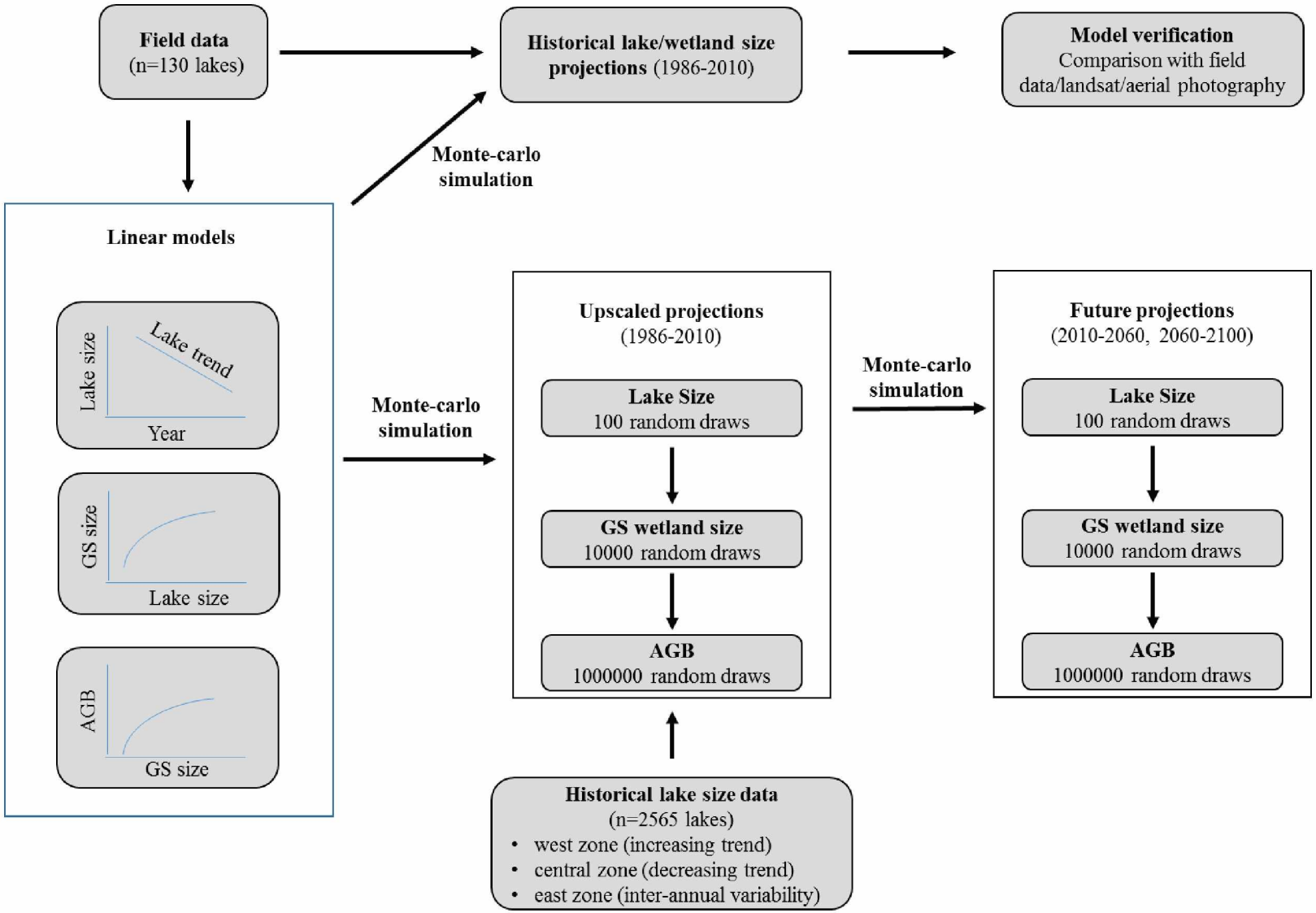

Figure 4.2. Flow diagram of multi-stage monte-carlo simulation. The diagram shows relationships between data sources, analyses, and objectives, for one wetland type (GS) and one wetland characteristic (AGB).

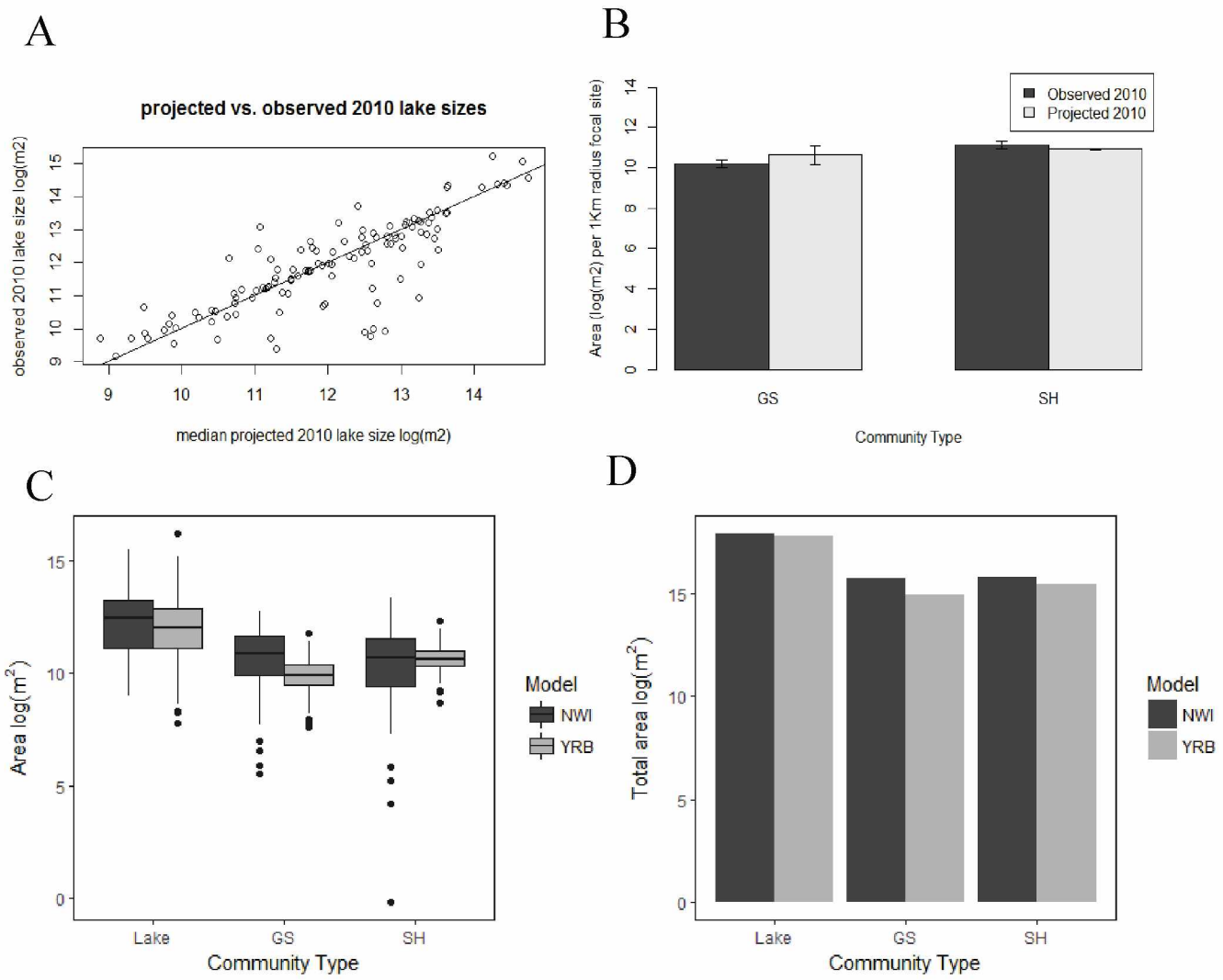

Figure 4.3. Lake and wetland size model verification. Top row: Projected and observed lake sizes (A) and grass/sedge (GS) & deciduous shrub (SH) wetland community sizes (B) for 130 field-sampled lakes in the Yukon Flats National Wildlife Refuge in 2010. Projected lake sizes are based on linear trends derived from 30 years of Landsat imagery, while projected wetland sizes are derived from projected lake sizes and linear models of wetland size as a function of lake size. The solid line in panel A represents the best fit line from a linear model of observed size as a function of projected size (ln(observed size) = 0.856*ln(projected size)+1.64, R2=0.66, $p < 0.0001$. In panel B, error bars represent 25th and 75th percentile of 10,000 simulated wetland sizes. Predicted and observed 2010 sizes were not significant for GS or SH communities (GS: t=0.23, df=137.41, p=0.82; SH: t=-0.93, df=232.05, p=0.35). Bottom row: Projected 1986 sizes of individual lakes and wetlands (C) were significantly different between National Wildlife Inventory (NWI) and Yukon Flats projections (YRB) for GS (t=3.31,df=117.07,p=0.001) but not for SH (t=-1.87,df=111.68,p=0.06) or Lake (t=1.44,df=238.54,p=0.15). Total area of 130 field-sampled lakes and wetlands were similar for NWI and YRB 1986 projections (D).

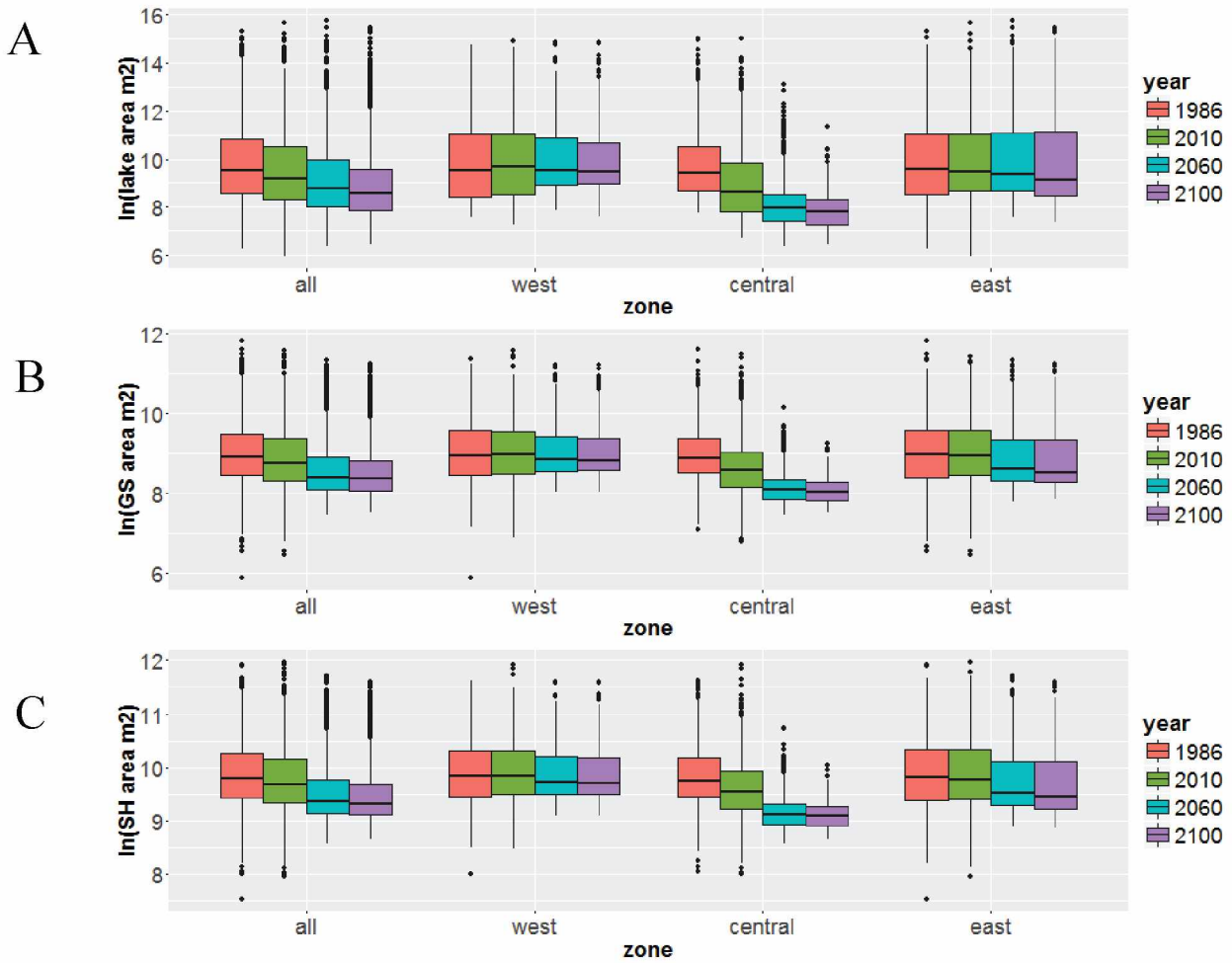

Figure 4.4. Lake and wetland area projections. Projected change in lake area (A) and lake-margin grass sedge (GS) and shrub (SH) wetland area (B, C) from 1986 to 2100. Boxes reflect median, 25th percentile, and 75th percentile of 100 simulations at each time period for lake sizes and 10,000 simulations for GS and SH area. Projections included all lakes in each of three zones (west, n=699; central, n=1129; and east, n=737) and all zones combined (n=2565).

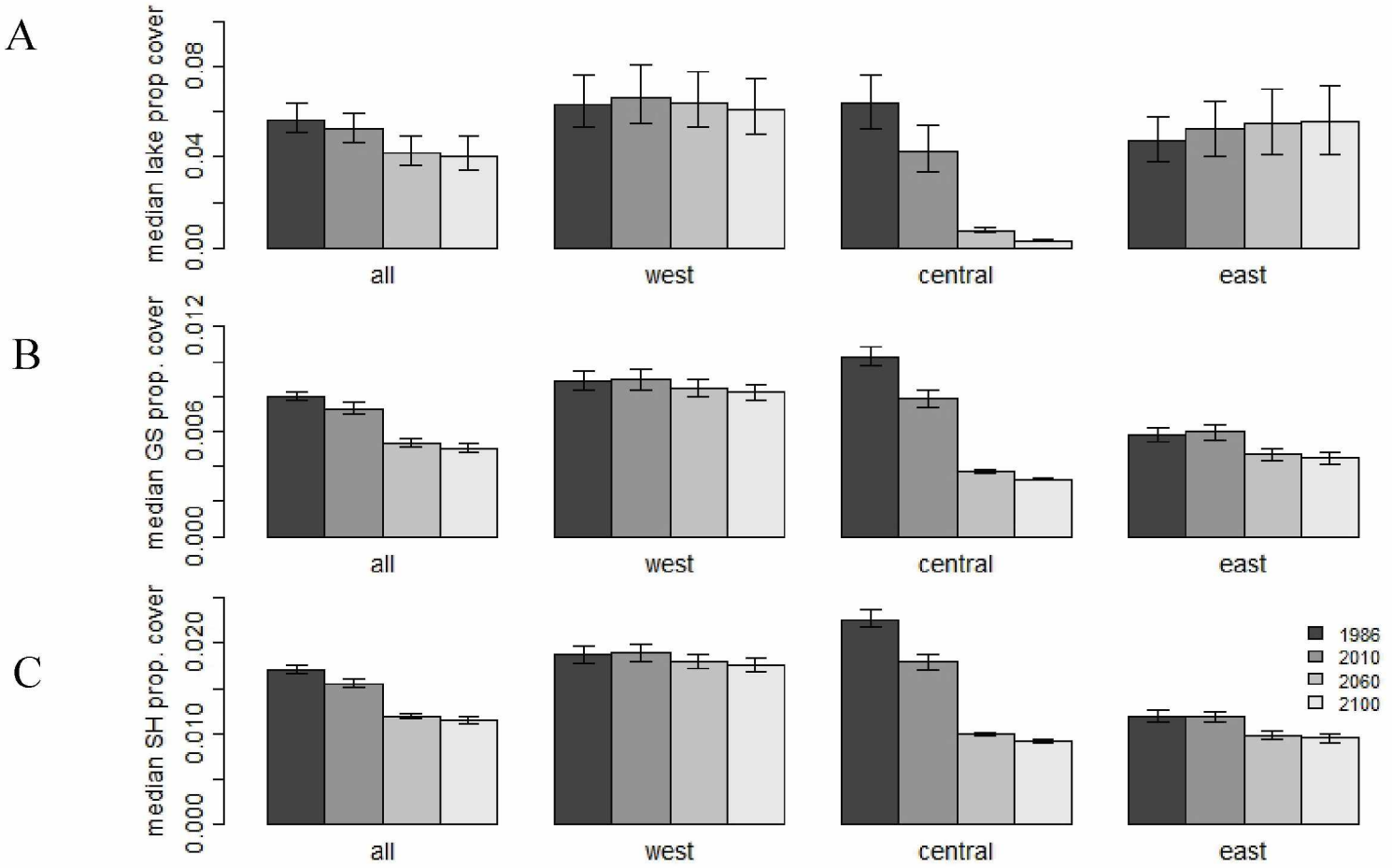

Figure 4.5. Lake and wetland total surface area projections. Projected change in the proportion of total surface area occupied by lakes (Panel A), grass/sedge wetlands (GS; Panel B) and shrub wetlands (SH; Panel C) from 1986 to 2100. Values are the median of 100 simulations at each time period for lake sizes and 10,000 simulations for GS and SH area. Projected values were summed across all lakes in each of three zones (west, n=699; central, n=1129; and east, n=737) and for all zones combined (n=2565). Error bars are 95% confidence intervals around the mean.

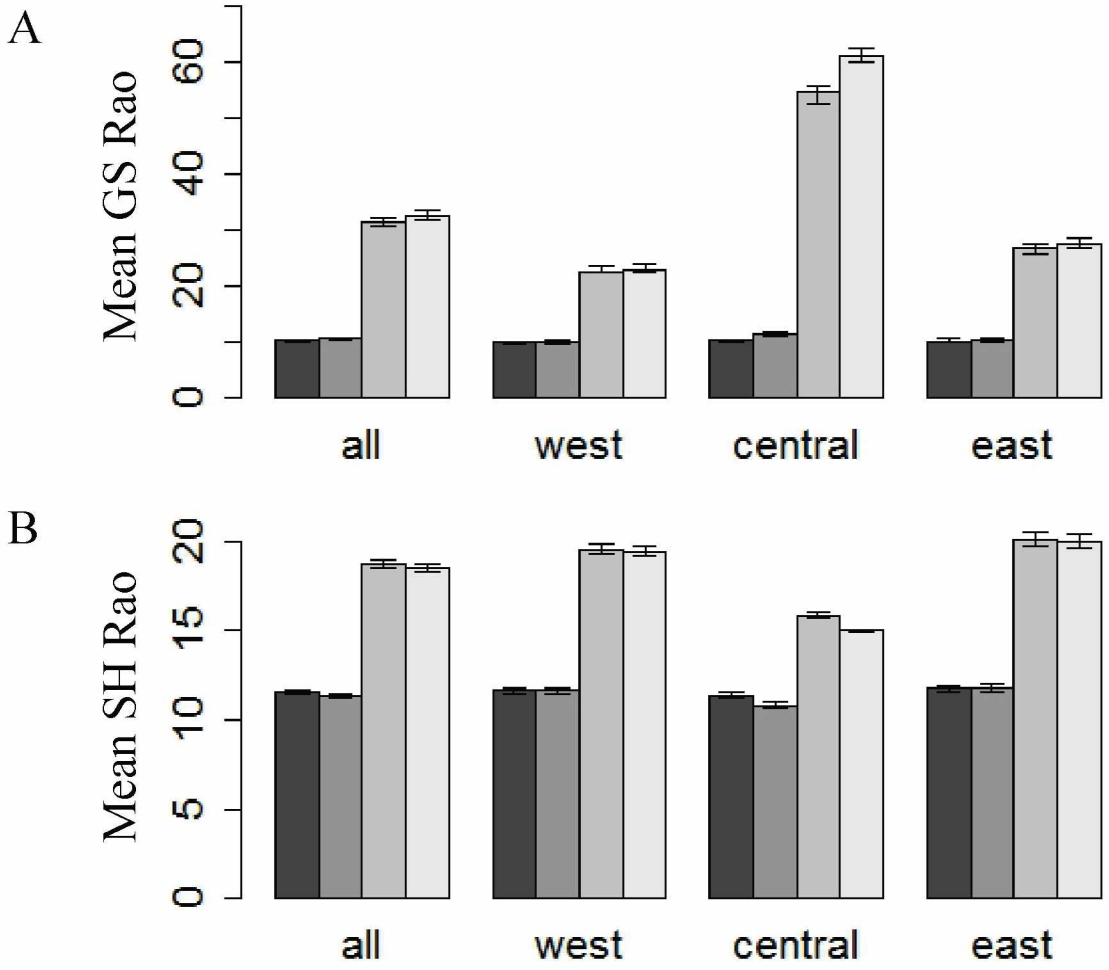

Figure 4.6. Functional diversity projections. Projected change in mean functional divergence scores, measured by Rao's quadratic entropy (Rao). Values at each time period are area-weighted means based on projected community size and projected Rao values at Grass/Sedge (GS; Panel A) and Deciduous Shrub (SH; Panel B) communities associated with each of 2565 lakes divided among three zones in the Yukon Flats National Wildlife Refuge (west, central, and east), and for all zones combined. Error bars are 95% confidence intervals around the mean.

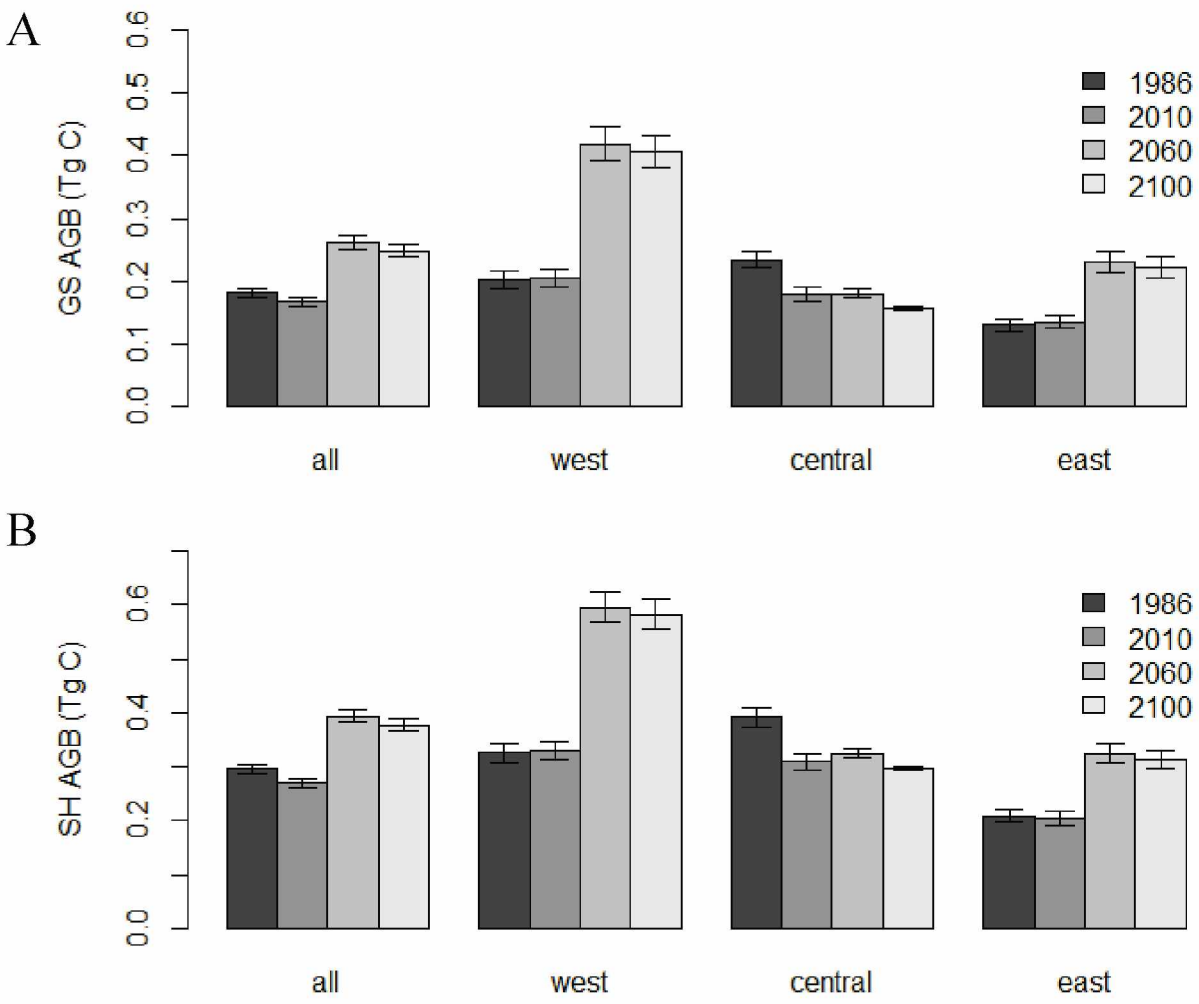

Figure 4.7. AGB projections. Projected change in mean total AGB per community type. Values at each time period are on based on projected change in community size and in AGB per m2 at Grass/Sedge (GS; Panel A) and Deciduous Shrub (SH; Panel B) communities associated with each of 2565 lakes divided among three zones in the Yukon Flats National Wildlife Refuge (west, central, and east), and for all zones combined. Error bars are 95% confidence intervals around the mean.

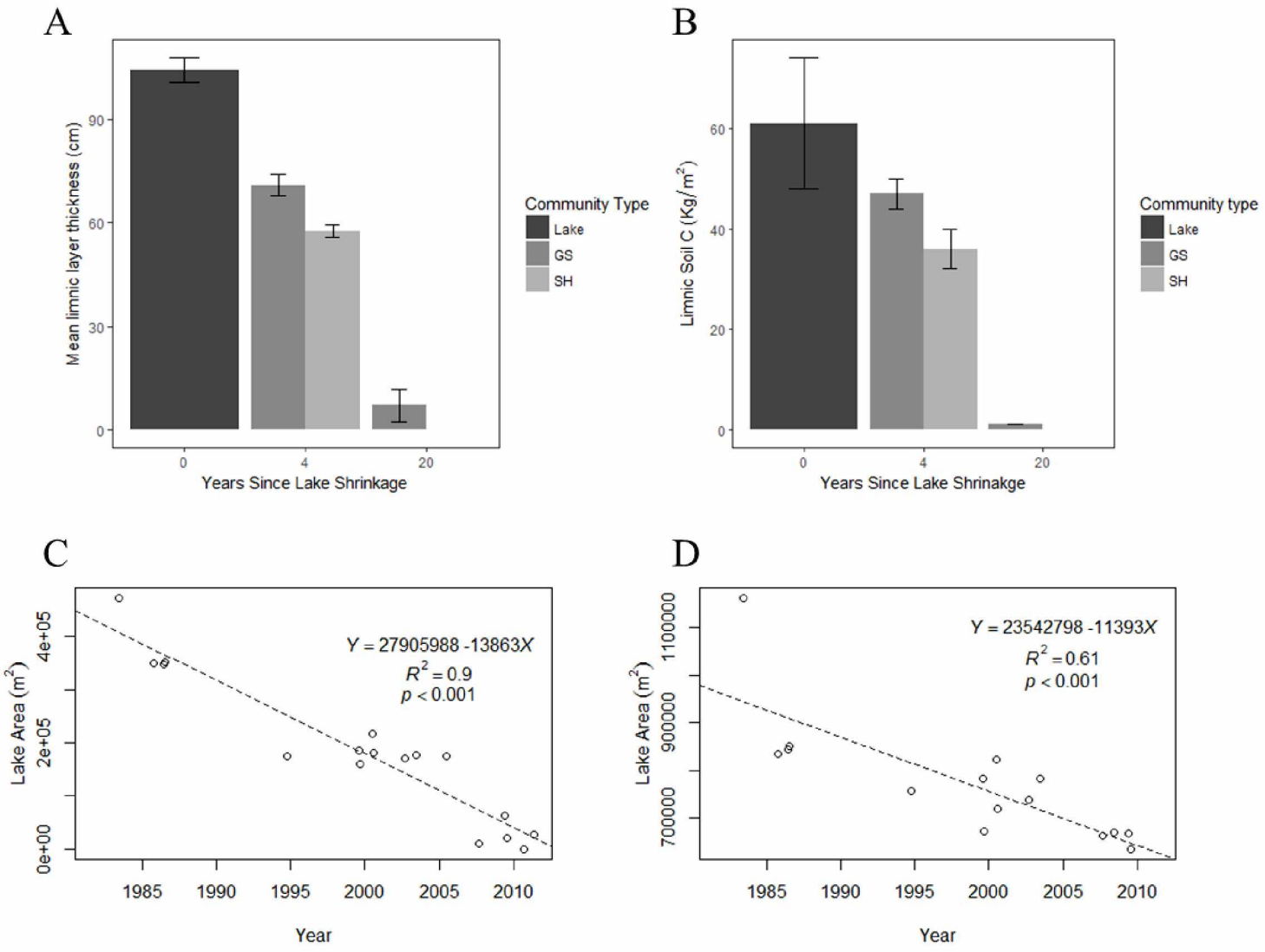

Figure 4.8. Limnic horizon chronosequence. The limnic horizon was cored down to mineral soil in the basin of a single rapidly drying lake (Lake 1_99_1) in the Yukon Flats National Wildlife Refuge, as well as in GS and SH wetlands at Lake 1_99_1 and at an adjacent lake that has shrunk more slowly (lake 1_99_2). All samples were collected in 2010. GS and SH wetlands at lake 1_99_1 occurred on soils exposed by lake shrinkage between 2005 and 2007 (Average age = 4 years), while GS and SH wetlands at Lake 1_99_2 were on soils exposed between 1986 and 1994 (Average age = 20 years). Top row: Average limnic horizon thickness (A) and Limnic C per m2 (B). Bottom row: linear regression models showing the historical change in lake size at Lake 1_99_1 (C) and Lake 1_99_2 (D). Best fit lines and equations are shown on each plot.

Table 4.1. Lake and wetland characteristics. Summary of lake and terrestrial plant community characteristics in the central lowlands of the Yukon Flats National Wildlife Refuge. Values are means and standard errors (in parentheses) for a spatially balanced random sample of 130 lakes, except for variables marked with an '*' which were estimated from field samples at a representative subsample of 14 lakes (6 Stable, 4 Shrinking, and 4 Fluctuating). Panel A contains lake-specific values, including fire history based digitized fire scars (https://fire.ak.blm.gov). Panel B describes common terrestrial plant communities including Grass/Sedge (GS), Deciduous Shrub (SH) and upland forest (F). Variable abbreviations are dissolved organic carbon (DOC), active layer thickness (ALT), above-ground biomass (AGB), soil organic carbon (SOC), and probability of having been burned within the last 50 years (p(burned w/in 50 years)). ^Lake Sediment C was estimated using a published linear relationship with lake size (Kortelainen et al. 2004).

A

Lake Type	Area (log m^2)	DOC log(mg /L)	^Lake Sediment C (Kg C /m^2)	p(burned w/in 50 years)
Stable	11.89 (0.16)	3.58 (0.09)	38.75 (0.07)	0.25 (0.05)
Shrink	11.48 (0.27)	3.63 (0.08)	40.73 (0.13)	0.09 (0.06)
Fluctuating	12.37 (0.35)	3.26 (0.13)	36.52 (0.14)	0.24 (0.09)

B

Community	Lake Type	Area (log ha)	ALT (cm)	AGB (Mg C / ha)	*Soil moisture (g H_20/g soil)	*SOC (Kg C /m^2)
GS	Stable	9.95 (0.26)	95.7 (0.61)	77.21 (15.71)	3.54 (2.41)	78.62 (26.63)
	Shrink	9.77 (0.45)	95.6 (1.35)	63.69 (10.74)	1.7 (0.6)	50.05 (15.31)
	Fluctuating	9.82 (0.67)	94.07 (1.11)	141.01 (39.34)	1.63 (0.61)	47.07 (12.01)
	All	9.77 (0.21)	94.79 (0.55)	87.32 (11.62)	2.49 (0.61)	46.46 (8.17)
SH	Stable	10.38 (0.27)	94.28 (0.79)	46.46 (4.08)	2.31 (0.54)	27.02 (3.65)
	Shrink	10.94 (0.17)	94.07 (1.44)	47.64 (8.37)	1.55 (0.21)	59.26 (25.19)
	Fluctuating	11.32 (0.48)	93.45 (1.11)	55.61 (13.35)	1.18 (0.39)	21.01 (6.4)
	All	10.6 (0.19)	93.68 (0.6)	49.3 (4.23)	1.76 (0.26)	25.4 (3.13)
F	All	-	93.32 (0.7)	44.09 (2.35)	1.32 (0.28)	20.86 (2.52)

Table 4.2. Wetland area linear models. Linear models of wetland area (log(area m2)) and odds of occurrence, predicted by lake area and rates of lake shrinkage. Models were fit based on remotely sensed estimates of lake size and field-derived measurements of wetland area from grass/sedge (GS) and deciduous shrub (SH) lake-margin wetlands in the Yukon Flats National Wildlife Refuge. Beta coefficients and standard errors (SE) are shown for the effects of lake area, lake shrinkage rate, and a lake area * lake shrinkage rate interaction term. ** indicates coefficient p-values < 0.0001, and * indicates coefficient p-values < 0.05. Occurrence/absence models were logistic regressions, and coefficients from those models are shown as back-transformed odds ratios. I also present overall model R2 and p values. These models were used to distinguish among alternative hypotheses about lake size, lake shrinkage rates, and rates of succession by lake-margin wetland vegetation.

		Independent variables									
Community	Predictor variable	log(lake area)	SE	shrinkage rate (log m^2/yr)	SE	Interaction	SE	Intercept	SE	R^2	
GS	log(area m^2)	0.44**	0.09	-	-	-	-	5.51**	1.133	0.22	<0.0001
GS	Presence odds ratio	-	-	-	-	-	-	3.96**	0.92	-	-
SH	log(area m^2)	0.32**	0.07	60.89*	30.26	-5.56*	2.58	7.44**	0.796	0.31	<0.0001
SH	Presence odds ratio	-	-	-	-	-	-	4.43**	1.11	-	-

Table 4.3. Linear models of lake and wetland characteristics. Linear model coefficients, root mean squared error, R2, and p values for top linear models of functional divergence (Rao), above-ground biomass (AGB, log(Mg/ha)), soil organic carbon (SOC, log(Kg/m2)), dissolved organic carbon (DOC, log(g/m3)), and lake organic sediment carbon (Lake Sed C, √(Kg/m2)) in three land cover types (Grass/Sedge (GS), Deciduous Shrub (SH), and Lake) in the central lowlands of the Yukon Flats National Wildlife Refuge, Alaska. Interaction terms are represented by a ':'. All models were fit using field data from a sample of 130 lakes, except for the relationship between Lake Sed C and lake area, which was developed by Kortelainen et al (2004).

Response	Community	Log (lake area m^2)	Log (GS area m^2)	Log (SH area m^2)	Intercept	Lake:GS	Lake:SH	RMSE	R^2	p
AGB	GS	0.16	-0.37	-	5.15	-	-	0.9	0.16	<0.0001
AGB	SH	0.12	-	-0.31	5.05	-	-	0.67	0.12	0.0008
RAO	GS	-1.16	-2	-	20.99	0.13	-	0.69	0.33	<0.0001
RAO	SH	0.15	-	-0.18	2.87	-	-	0.57	0.08	0.05
SOC	GS	0.07	-	-	1.55	-	-	0.33	0.07	0.04
SOC	SH	-	-	-	2.53	-	-	0.33	-	-
DOC	Lake	-0.07	0.13	-0.16	4.73	-	-	0.58	0.31	<0.0001
Lake Org Sed C	Lake	0.4	-	-	10.9	-	-	0.62	0.47	nr

Appendix B. Projected changes in C storage associated with land cover change driven by shrinking lakes

Introduction/Methods

C stock projections have been included as a supplement to the lake and wetland projections contained in Chapter 4. These projections were derived from a multi-stage Monte Carlo model that used statistical relationships between lake size, wetland size, and lake and wetland C stock densities, to project change in C storage associated with shrinking lakes and wetlands. See Chapter 4 for a detailed description of the model framework and data collection methods. Lake trend estimates came from three zones within the Yukon Flats National Wildlife Refuge. Projections of above-ground biomass (AGB), soil organic carbon (SOC), dissolved organic carbon in lake water (DOC), and lake sediment organic C (Lake Org Sed C) were derived for two wetland types: Grass/Sedge (GS), and Shrub (SH). To assess whether C losses could be recovered through the replacement of lake and wetland area with upland forest, I multiplied the total area of lake and wetland area lost between 1986 and 2100 (e.g. the area occupied by new upland forest), by estimates of AGB and SOC per m^2 of upland forest, and added these estimates to the total 2100 lake/wetland C stock projections. Forest AGB and SOC/OLT measurements were collected along with GS and SH data at field-sampled lakes, using the same methods.

These projections relied on 3 major assumptions: 1) Wetland soil C density per m^2 was stable over time. 2) Limnic (lake sediment) C stocks were highly labile and would be rapidly decomposed within decades after the encroachment of wetland vegetation into former lake beds. 3) The observed relationship between lake sediment C density per m^2 and lake size in boreal

Finland, as described in Kortelainen et al. (2004), reflected a universal property of boreal lakes, and could be used to predict lake C stocks in Alaska. The first of these assumptions is likely to be violated as a general rule, but field data from the Yukon Flats and elsewhere in Alaska were consistent with the idea of lake sediment C stocks that were larger, and potentially more labile, than the organic soil C stocks in lake-margin wetlands (Jorgenson et al. 2013; Chapter 4). This appendix was meant to provide a first-order estimate of the potential change in these large and vulnerable C stocks, due specifically to shrinking lake sizes.

Results

Upscaling from all zones combined, my models estimated the total size of the 2010 lake/wetland organic C pool in the study area as 21.31 Tg C (CI=19.32-23.36). This pool was projected to shrink by 32% between 1986 and 2100 for all zones combined, from 23.37 Tg C (CI=21.44-25.29) in 1986 to 16.40 Tg in 2100 (CI=14.45-18.53; Fig. B.1). This decline was driven mainly by a large projected decline in the Central zone, which represents the most extreme lake shrinkage scenario currently observed in Alaska. Lake sediment organic C was the largest single stock, and was larger than all other stocks put together in all zones and times except the central zone, where it shrank to only 1.86 Tg (CI=1.77-1.96) in 2100, representing 49% of the total organic C pool (Fig. B.1). When total stocks for all zones combined were upscaled to the size of the whole study area, total lake sediment organic C was projected to shrink from 19.89 Tg (CI=18.07-21.68) to 13.7 Tg (CI=11.94-15.82) from 1986-2100 (Fig. B.1B). In the models I applied, lake sediment organic C was quadratically related to lake size (Table 4.3), with a peak C density at lakes between 1 and 10 ha (Kortelainen et al. 2004).

Unlike lake sediment C, DOC increased from 1986 to 2010 before declining in future projections for all zones (Fig. B.1C). The top model for DOC, used to generate these projections, identified lake size, GS area, and SH area as all being important but contradictory predictors; Lake and SH size were both negatively correlated with DOC, but DOC was positively correlated with GS size (Table 4.2, Table 4.3). For upscaled projections from all zones combined, DOC was consistently the smallest individual stock, with a mean current projected value of 0.013 Tg (CI=0.011-0.15) in 2100, and represented less than 1% of total organic C stocks in all scenarios (Fig. B.1C). The largest drop in total DOC occurred in upscaled projections from the western (increasing lake) zone between 1986 (0.052 Tg, CI=0.044-0.060) and 2100 (0.036 Tg, CI=0.031-0.043; Fig. B.1C).

SOC per m^2 was not well predicted by lake or wetland size in either GS or SH communities (Table 4.2, Table 4.3). Although there was a significant relationship between GS SOC and lake size in my field-sampled lakes dataset, this relationship had an R^2 of only 0.07. However, projected decreases in total GS and SH area over time were associated with a 34% decrease in the wetland SOC pool for all zones combined between 1986 (upscaled mean = 3.00 Tg, CI=2.90-3.10) and 2100 (upscaled mean= 1.97 Tg, CI=1.90-2.05; Fig. B.1C). Total SOC was stable over time in the western (increasing lakes) zone, but decreased by 20.6% in the eastern (fluctuating lakes) zone (1986 mean = 2.13, CI=1.99-2.27; 2100 mean = 1.69, CI=1.58-1.80). In the central (rapid shrinking) zone, total SOC was estimated to decrease by 63.5% (1986 mean = 3.92, CI=3.72-4.11; 2100 mean = 1.42, CI=1.40-1.45; Fig. B.1C). The GS SOC pool was approximately 40% the size of the SH pool in most scenarios and years (mean for all zones combined across all years, upscaled to whole study area = 39%, CI=35-42%, but in the central zone, the GS SOC pool declined to only 24% of the SH pool by 2100 (CI=24-25%; Fig. B.1C).

Soil cores reached mineral soil at all but a handful of lakes, so SOC estimates included the majority of limnic sediments still present in wetland soils.

For all zones combined, the organic C pool stored in freshwater stocks (DOC and lake organic C), was five to six times as large as the total terrestrial wetland pool (AGB and SOC) throughout the projection period (mean freshwater: terrestrial total C ratio for all years = 5.51, CI=5.12-5.90). However, for the eastern zone, the freshwater: terrestrial C ratio increased over time, from 6.45 (CI=5.73-7.24) in 1986 to 7.96 (CI=6.84-9.24) in 2100. In the central zone, the ratio of freshwater to terrestrial C pools dropped from 5.08 (CI=4.6-5.6) in 1986 to 1.0 (CI=0.97-1.04) in 2100, reflecting the projected decrease in lake surface area and its relationship to projected lake sediment C. The western zone freshwater:terrestrial C ratio decreased slightly from 1986 (mean=5.86, CI=5.32-6.39) to 2100 (mean=5.27, CI=4.68-5.84).

Decreases in total organic C over time were not compensated by the conversion of lakes and wetlands to upland forest between 1986 and 2100. The C pool represented by new upland forest replacing lake and wetland area in in all zones combined, upscaled to the whole study area, was projected to be 2.24 Tg C (CI=1.95-2.53) (Fig. B.2). These additions represented about a third of the lake and wetland C lost during the same period (Fig. B.2).

Discussion

Total Lake C stocks

In terms of projected C stocks, I did find support for the hypothesis that lake shrinkage would decrease the total amount of organic C stored in lakes and wetlands. The magnitude of this decrease was projected to be more than twice as large in the central scenario as in all zones combined (Fig. B.1). As I predicted, the largest stock, organic lake sediment C, was by far the

most sensitive to projected declines in lake size over time, especially in the central zone. The comparison of lake C projections to my other analyses is challenging, because it was the only stock estimated using published data from outside my study area. However, the lake C model that I used was derived from a large, widely distributed sample of Finnish lakes from latitudes similar to my study area, and it explained almost half of all variability in lake sediment C per unit area in that dataset (Kortelainen et al. 2004). In addition, similar relationships between lake area and organic sediment C have been documented around the world (Ferland et al. 2012), and lake sediment C estimates from the Kortelainen model were within 1 standard error of the average C density in the single lake basin I sampled (Chapter 4). If anything, comparisons with multiple North American and European study sites implied that my approach probably yielded a conservative estimate of the size of the lake sediment C stock (Ferland et al. 2012). My estimate of the loss in C stocks represented by the conversion of lakes to terrestrial wetlands was also based on the assumption that changes in soil characteristics rapidly follow changes in land cover and water table depth associated with lake shrinkage (Sulman 2012). However, this assumption was supported by experimental/empirical evidence that the organic matter in exposed limnic sediments is extremely labile and vulnerable to rapid microbial decomposition (Jorgenson et al. 2013; Chapter 4).

DOC

DOC stayed relatively stable over time in all zones as lakes and wetland size decreased, a result that was consistent with my initial predictions. DOC in boreal lakes is derived primarily from terrestrial sources, and was positively associated with GS wetland size (Chapter 2) (Larmola et al. 2004; Mattsson et al. 2005; Benoy et al. 2007). Since lakes shrunk more rapidly than GS wetlands in my central zone projections, leading to an increase in the ratio of total GS

area to total lake area, it is not surprising that DOC would be buffered against the effects of lake shrinkage. In addition, DOC concentrations were correlated with maximum lake depth, a variable that was not significantly correlated with lake size in my study area (Chapter 2; Read et al. 2015). As discussed in Chapter 2, the association between DOC and depth suggested that DOC concentrations were affected not only by inputs of terrestrial organic matter, but also by microbial consumption of that material within a lake.

DOC was consistently the smallest of all C stocks, making up less than 1 percent of the total organic C pool, but my results likely underestimated the importance of DOC as a component of the C budget. Most of the DOC leached into boreal lakes from surrounding wetlands is transmitted in a large spring pulse, and the majority of this pulse is rapidly consumed by microbes and released into the atmosphere as CO_2 (Chapter 2) (Larmola et al. 2004; Benoy et al. 2007). Boreal lakes are typically supersaturated with CO_2, and this flux is several times larger than the rate of particulate organic accumulation in lake sediments (Cole et al. 1994; Kortelainen et al. 2013). My DOC projections probably represented only the small concentration that remains by mid to late summer, when my data were collected. It is also unclear how much of the DOC in lake and wetland waters in the Yukon floodplain is ultimately exported to the Yukon River itself and transported to the Bering Sea. Summer DOC export in the Yukon has declined over the last few decades, and these declines have been associated with a reduction in the proportion of surface water vs. groundwater inputs (Walvoord and Streigl 2007). Reductions in the area of wetlands in the Yukon River watershed could further reduce DOC export to the river, although reductions in lake area could mean that less terrestrial DOC is intercepted and processed by lake microbes before reaching the river. Tracing the fate of DOC derived from terrestrial sources throughout the growing season is an important area for future research, especially since a

significant fraction of lake C is converted to methane, a more potent greenhouse gas than CO_2, before being vented to the atmosphere (Bastviken et al. 2004). Smaller boreal lakes produce significantly more methane and CO_2 per m^2 than larger ones, and emissions are positively correlated with wetland area. As a result, methane and CO_2 emissions are sensitive to the effects of lake and wetland shrinkage (Bastviken et al. 2004; Juutinen et al. 2009; Kortelainen et al. 2013).

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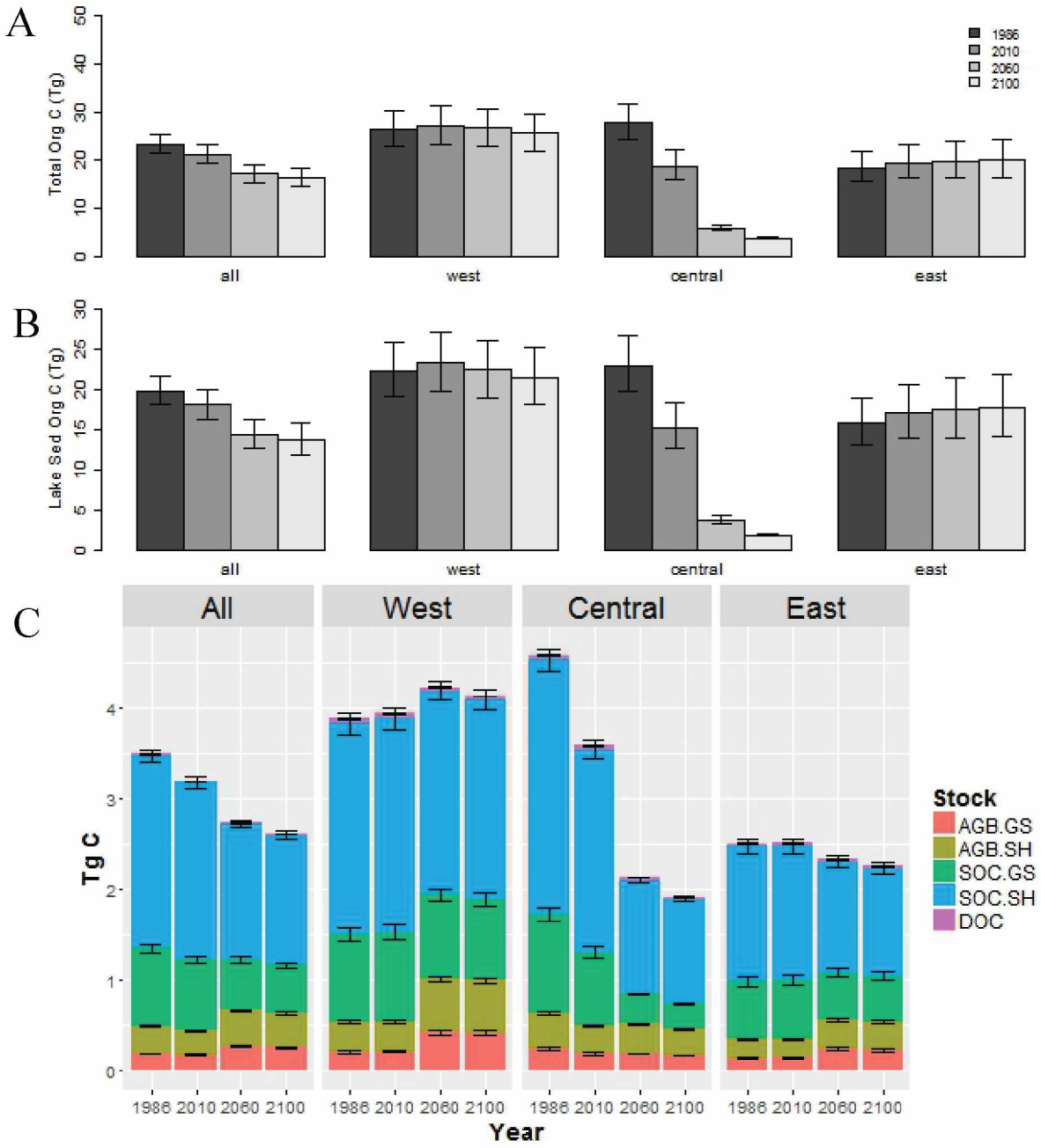

Fig. B.1. Mean projected change in aquatic and terrestrial organic C stocks in the central lowlands of the Yukon Flats National Wildlife Refuge. Values are the average of lake- or wetland-specific estimates weighted by area. Panel A : Total Organic C, Panel B: Lake Sediment Organic C, Panel C: All other stocks. These include Above-ground Biomass (AGB) and soil organic C (SOC) for grass/sedge (GS) and shrub (SH) communities, and lake dissolved organic C (DOC). Projections are shown for each of three zones (west, central and east) and for all zones combined. In each case, values were normalized to the whole study area by multiplying total zone stocks by the ratio (study area size/zone size), to allow for easy comparison and to illustrate the potential consequences if lake trends in any one zone were to become representative of the whole study area. Error bars are 95% confidence intervals for the mean.

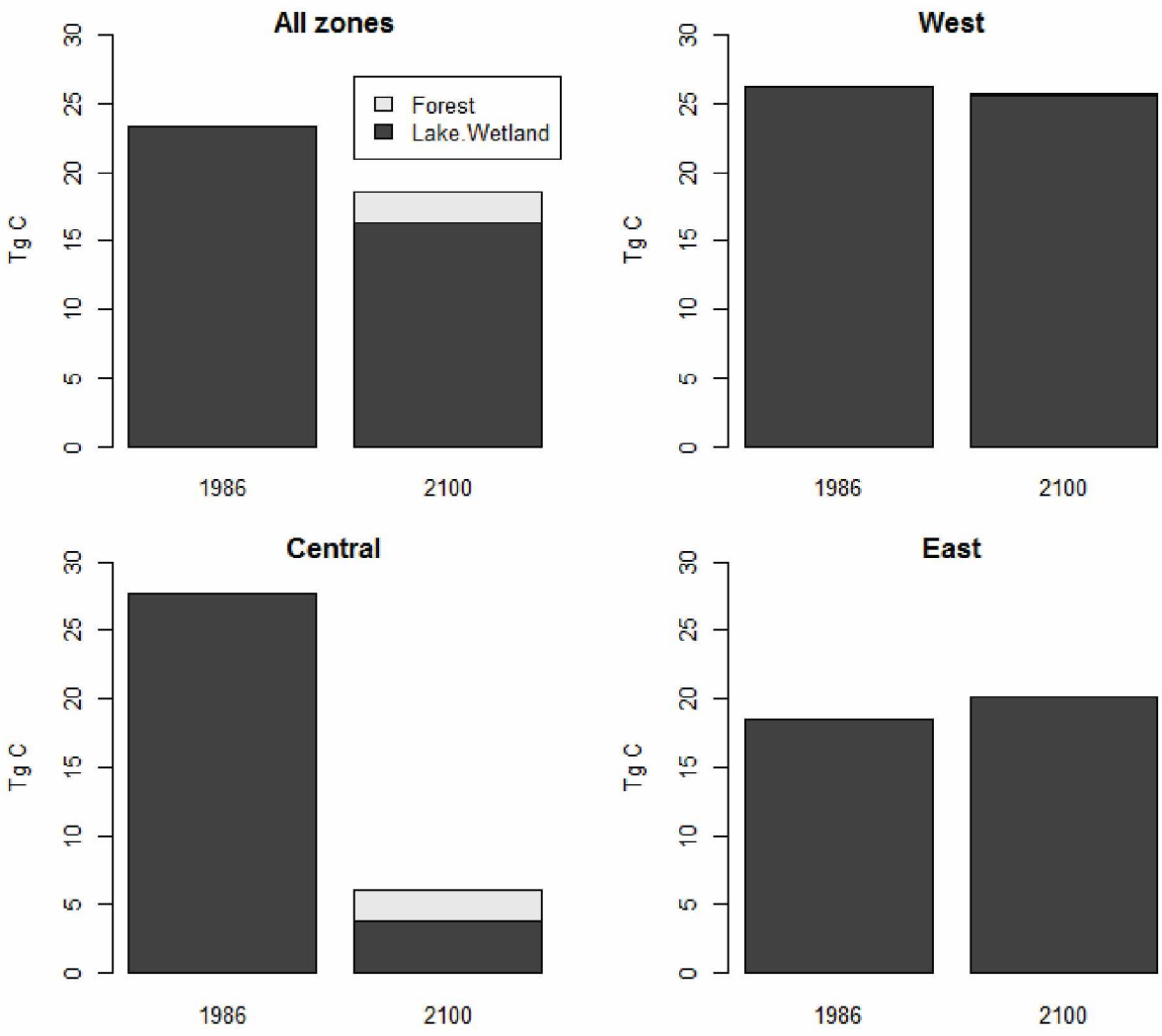

Fig. B.2 Comparison of total 1986 lake and wetland organic C stock with projected lake and wetland stocks in 2100, and estimated size of the organic C stock represented by lakes and wetlands converted to upland forest.

Appendix C. Mean vegetation and soil characteristics for Yukon Flats lacustrine plant communities.

Table C.1. Vegetation community characteristics. Values were averaged from samples collected at 14 lakes between 2010 and 2011. Values include Specific Leaf Area (SLA), above-ground biomass (AGB), net primary production (NPP) and carbon:nitrogen ratios (CN), for 9 plant functional types (PFT). Values are shown for 4 plant community types: Grass/Sedge wetland (GS), Deciduous Shrub wetland (SH), Coniferous Forest (CF), and Deciduous Forest (DF).

Community	PFT	SLA*	% cover	AGB (g C/m^2)		NPP (g C/m^2)			CN	
				L	W	L	W	R	L	W
GS	Dec shrub†	0.017	8.09	34.54	25.99	32.78	14.22	-	24.07	63.37
	Ev shrub	0.015	5.81	-	-	-	-	-	30.28	53.64
	Dec tree	0.011	2.78	-	-	-	-	-	32.52	63.37
	Ev tree	0.011	2.78	0.45	-	0.36	-	-	36.41	77.72
	Forb	0.02	20.54	117.77	-	55.21	-	-	32.3	-
	Gram	0.017	65.08	737.81	-	187.29	-	-	35.34	-
	Lichen	-	5.66	37.88	-	12.83	-	-	28.83	-
	NS moss	-	4.44	82.36	-	40.95	-	-	26.1	-
	Equisetum	0.009	16.02	163.84	-	72.73	-	-	22.84	-
	All	-	-	-	-	-	-	20.77	-	-
SH	Dec shrub†	0.017	52.02	50.91	87.33	34.87	8.05	-	24.07	63.37
	Dec tree	0.015	6.96	23.05	26.03	13.18	0.36	-	30.28	53.64
	Ev shrub	0.011	5.81	35.94	1000.19	34.31	36.91	-	32.52	63.37
	Ev tree	0.011	6.96	156.12	919.68	128.96	26.79	-	36.41	77.72
	Forb	0.02	14.2	6.83	-	4.32	-	-	32.3	-
	Gram	0.017	22.78	259.09	-	105.83	-	-	35.34	-
	Lichen	-	5.32	4.44	-	4.2	-	-	28.83	-
	NS Moss	-	8.18	67.39	-	22.46	-	-	26.1	-
	Equisetum	0.009	8.16	2.38	-	2.08	-	-	22.84	-
	All	-	-	-	-	-	-	18.88	-	-

Table C.1 continued. Vegetation community characteristics. Values were averaged from samples collected at 14 lakes between 2010 and 2011. Values include Specific Leaf Area (SLA), above-ground biomass (AGB), net primary production (NPP) and carbon:nitrogen ratios (CN), for 9 plant functional types (PFT). Values are shown for 4 plant community types: Grass/Sedge wetland (GS), Deciduous Shrub wetland (SH), Coniferous Forest (CF), and Deciduous Forest (DF).

Community	PFT	SLA	% cover	AGB (g C/m^2)		NPP (g C/m^2)			CN	
				L	W	L	W	R	L	W
	Dec shrub†	0.017	21.56	36.52	23.25	23.32	3.86	-	24.07	63.37
	Dec tree	0.015	0	31.76	698.55	26.7	17.1	-	30.28	53.64
	Ev shrub	0.011	20.95	23.54	6.21	10.61	1.54	-	32.52	63.37
	Ev tree	0.011	46.51	445.06	2896.03	53.15	89.52	-	36.41	77.72
	Forb	0.02	10.01	7.97	-	6.25	-	-	32.3	-
	Gram	0.017	6.62	15.34	-	3.29	-	-	35.34	-
	Lichen	-	11.92	4.29	-	0.39	-	-	28.83	-
	NS moss	-	28.56	78.12	-	40.95	-	-	26.1	-
	Equisetum	0.009	4.33	13.23	-	11.81	-	-	22.84	-
	All	-	-	-	-	-	-	15.74	-	-
DF	Dec shrub†	0.017	29.44	76.95	66.15	34.84	9.88	-	24.07	63.37
	Dec tree	0.015	26.75	102.57	2508.12	47.09	43.25	-	30.28	53.64
	Ev shrub	0.011	26.29	4.86	24.78	5.82	1.89	-	32.52	63.37
	Ev tree	0.011	26.75	272.68	1116.36	8.79	43.74	-	36.41	77.72
	Forb	0.02	12.27	13.03	-	29.99	-	-	32.3	-
	Gram	0.017	12.28	68.2	-	27.57	-	-	35.34	-
	Lichen	-	8.21	15.92	-	1.96	-	-	28.83	-
	NS moss	-	9.96	187.02	-	111.66	-	-	26.1	-
	Equisetum	0.009	3.02	0.36	-	0.36	-	-	22.84	-
	All	-	-	-	-	-	-	15.74	-	-

† Salix/Betula abundance percentages for AGB and NPP were CF: (1/0), GS: (87/13), SH: (53/47), and DF: (80/20).

Chapter 5 : Conclusion

The research described in this thesis supports the hypothesis that climate-mediated lake shrinkage has widespread effects on terrestrial and aquatic boreal ecosystems. I presented evidence that ecohydrological interactions between boreal lakes and lake-margin wetlands operate in both directions, and include exchange of water, organic matter, nutrients, and C. These exchanges are a significant influence on ecologically and socially valuable lake and wetland characteristics, including biodiversity, wildlife habitat quality, primary productivity, water chemistry, and C storage. The effects of long-term changes in lake area can be seen at the landscape scale as well as at individual lakes and wetlands. However, I also found that the effects of lake area change could be moderated or overwhelmed by other physical variables, including wildfire history and lake geomorphology, and by biotic factors including succession and its effect on the functional role of vascular plant communities. Moreover, lake shrinkage can have simultaneous positive and negative effects on different ecosystem properties, such as increased plant biodiversity combined with decreased C storage. Biotic and abiotic interactions between water and vegetation are important for understanding the current and future consequences of climate change (Rodriguez-Iturbe 2000), including changes in the structure and function of boreal landscapes (Roach et al. 2011). However, ecohydrological interactions can be challenging to study due to their complexity and their operation at multiple scales. My conclusions were based largely on a large-scale space-for-time substitution model, which had weaknesses relative to experimental approaches. However, the space-for-time model I developed made it possible to explore ecosystem responses to shrinking lakes at large spatial and temporal scales (Walker et al. 2010; Blois et al. 2013). Cumulatively, my results provided a novel picture of a landscape shaped by multiple drivers. Individual chapters quantified interactions between these drivers, while estimating uncertainty associated with their effects. I also highlighted relevant knowledge gaps

to prioritize for future research, and sought to present each analysis in terms of its management implications.

My results were broadly consistent with a large body of literature demonstrating the influence of watershed characteristics on lake ecosystems (Gergel et al. 1999; Grimm et al. 2003; Read et al. 2015). For example, in Chapter 3 I demonstrated that N loads, conductivity, and dissolved organic C in Yukon Flats lakes were significantly correlated with the size of adjacent herbaceous wetlands, which suggests that terrestrial organic matter was a substantial source of in-lake nutrients (Gergel et al. 1999). However, I also found that nutrient and ion concentrations in lake water were influenced by characteristics of the lakes themselves, especially bathymetry, which was related to water residence time. Lake shrinkage had multiple effects on lake nutrient dynamics: small, shallow lakes were more likely to be hyper-eutrophic, but water chemistry appeared to be less affected by inputs of organic matter in shrinking lakes compared to stable ones (Chapter 3).

I also found evidence of lake dynamics affecting terrestrial wetland characteristics. Herbaceous and woody lake-margin wetlands were distributed along a gradient of soil moisture, which decreased with increasing distance from the lake shore (Chapter 4). In Chapter 4, space-for-time substitution modeling suggested that lake shrinkage was followed by succession and a net loss of lake-margin wetland area within 30 years. In addition, compared to wetlands near stable lakes, wetlands near shrinking lakes were characterized by drier soils and supported more shrub-dominated plant communities with higher species richness, plant functional diversity, and greater AGB (Chapter 2; Chapter 4). All of these patterns were consistent with the hypothesis that lakes exerted a significant influence on wetland plant communities via their effects on the water table and soil moisture (Klein et al. 2005; Whitehouse and Bayley 2005; Sulman 2012)

Although I presented evidence for a variety of significant responses to long-term lake area change, there was a second broad theme running through each chapter in this dissertation. Specifically, the effects of lake area change were context-dependent, and could be mitigated, amplified, or overwhelmed by the simultaneous influence of wildfire, land-cover, geomorphology, and biotic effects related to biodiversity and community composition. In Chapter 2, I used structural equation modeling to untangle the effects of these interacting variables on wetland C storage, and found that the effects of lake shrinkage on wetland characteristics appeared to be independent of wetland responses to wildfire. However, the effects of lake shrinkage on wetland above-ground biomass (AGB) appeared to be mediated by interactions between lake size, wetland size, and plant functional diversity (Chapters 2 and 4). In addition, wetland AGB and soil organic layer thickness (OLT) were more strongly correlated with fire history, and with functional characteristics of wetland plant communities (e.g. functional diversity, idiosyncratic species, woodiness, growth rate, drought tolerance), than with rates of lake shrinkage *per se* (Chapter 2).

In Chapter 3, I used random forest modeling to examine the interactive effects of landscape variables, including wetland characteristics, on lake water chemistry and nutrient status. More than half of observed variability in lake dissolved organic carbon (DOC), dissolved nitrogen, and conductivity could be accounted for by a combination of land cover (specifically, the size of adjacent herbaceous wetland communities) and variables that described lake geomorphology and water residence time. In particular, in-lake concentrations of DOC and N were driven by organic matter input from lake-margin herbaceous wetlands and were positively correlated with herbaceous wetland size. These relationships between dissolved organic compounds and wetlands size implied that the loss of wetlands through drying and succession

could significantly alter nutrient and C cycling in boreal lakes (Chapter 3). The effects of lake area dynamics on water chemistry were best explained as the indirect result of reduced subsurface hydrologic connectivity (shrinking lakes) or increased surface water exchange (flooding lakes) between lakes and their surroundings (Chapter 3).

Because long-term changes in lake area have complex consequences for lakes and wetlands, the management of drying boreal landscapes may require tradeoffs to maximize the present and future value of protected lands. For example, the Yukon Flats is renowned for providing breeding habitat to millions of waterfowl every summer, and waterfowl species richness will likely decrease as individual lakes and wetlands continue to shrink (Roach and Griffith 2015). However, smaller, narrower bands of wetland vegetation in the YFNWR supported more species-rich vascular plant communities, and tended to produce more biomass per unit area, specifically woody browse that could provide high-quality forage for moose and other herbivores (Chapters 2 and 4). Similarly, aboveground plant biomass and belowground C storage had divergent responses to disturbance history, lake shrinkage rates, and plant community characteristics. These trends suggested that continued warming and lake shrinkage will likely have simultaneous positive effects (increasing plant diversity and relative abundance of woody browse) and negative effects (reduced waterfowl diversity and soil C storage). As a result, continued widespread lake shrinkage will pose a considerable management challenge for lands in the National Wildlife Refuge system, including the YFNWR, whose stated purpose is to preserve the "Natural diversity of fish, wildlife… and their habitats" (USFWS 1987). It may be prudent to address this challenge by considering local lake area trends and their implications for wetland structure and function when negotiating future land exchanges and other conservation measures in the YFNWR and other boreal refuges.

From an applied perspective, the greatest consequence of widespread lake shrinkage is possibly its potential to affect land cover by altering the size and relative abundance of lakes and wetlands across boreal landscapes. Exposed sediments in the margins of shrinking lakes were rapidly colonized by wetland and upland forest vegetation (Chapter 4). While wetland vegetation currently occurs in high-moisture nearshore soils surrounding most lakes in the study area, the net effect of lake shrinking and succession over the next century could be a roughly 35% decline in total wetland area (Chapter 4). However, there was considerable uncertainty surrounding these estimates, and projections of future lake and wetland size distributions spanned several orders of magnitude.

Sources of error/suggestions for future research

My results provide a starting point for assessing the relative effect of lake shrinkage on land cover, relative to wildfire and other forms of disturbance that help shape boreal landscapes (O'Donnell et al. 2011; Lewis et al. 2014). The land cover change projections in Chapter 4 may be improved through the use of process-based modeling. A comparison between field data and output from mechanistic simulation models would clarify the relative importance of various biological and phyiscal mechanisms (e.g. temperature- and moisture-driven changes in plant growth and organic matter decomposition) of lake-wetland dynamics (Rastetter 1996). My ability to project change in C storage was also severely limited by a lack of Alaskan lake sediment C stock measurements (Chapter 4). However, assuming that current lake area trends persist indefinitely, that Alaskan lakes are similar to European boreal lakes in their C storage capacity, and that limnic soils exposed by shrinking lakes can be decomposed within decades to centuries (Chapter 4), the rapidly drying central Yukon Flats could undergo an order-of-

magnitude reduction in organic C storage by 2100 due to widespread conversion of boreal lakes to wetlands (Appendix B).

The potential magnitude of the changes in wildlife habitat availability, biodiversity, and C stocks that could result from widespread lake shrinkage, as well as the wide error bars and strong assumptions associated with my projections, point to several priorities for future research. First, my work would have benefited greatly from the availability of remotely sensed maps of past and present vegetation, which would have allowed me to model rates of vegetation change with the methods I used to estimate trends in lake area. Unfortunately, as discussed in chapter 4, lowland boreal vegetation types cannot reliably be distinguished using multispectral data, and maps based on aerial photography (e.g. the National Wetlands Inventory or NWI; Wilen et al. 1995) are only available for one or two points in time. Additionally, the NWI has not been validated with field data for boreal lowland regions similar to the Yukon Flats, making it difficult to gauge the map's accuracy. A second problem plaguing my analysis, the lack of data on Alaskan lake sediment C stocks, could be remedied by an intensive sampling effort, as has been done in Finland. Lake C sequestration rates were incorporated into recent efforts to quantify Alaskan C budgets (Zhu and McGuire 2016) but measurements of total limnic sediment C stocks remain sparse. The vulnerability of this important C stock could be further evaluated by extending my efforts to sample lake sediments along a chronosequence of time since exposure to aerobic conditions (see Chapter 4).

Finally, the effects of lake shrinkage on ecosystem properties such as primary productivity and C flux would be best addressed by using my field data to inform a new class of integrated terrestrial-aquatic ecosystem models. To that end, I have included field estimates of commonly used ecosystem model parameters for boreal lake-margin plant communities in an

appendix to this dissertation (Appendix C). At the same time, the empirically derived projections of past and future landscape change that were presented in this study should provide a useful point of comparison for assessing the plausibility of deterministic simulation models and their outputs.

Final thoughts

High latitudes have warmed twice as rapidly as the rest of the world, and this warming trend is likely to continue (Hinzman et al. 2005). However, temperature trends alone provide an incomplete picture of climate change and its effects, because they fail to capture positive and negative feedback mechanisms, including changes in albedo due to loss of sea ice and snow cover (Curry et al. 1995; Euskirchen et al. 2007), thawing permafrost C stocks (Schuur et al. 2015), increased methane production from lakes and wetlands (Juutinen et al. 2003; Zhuang 2004), and shifting land cover (Dial et al. 2016). Water is fundamental to each of these mechanisms, because it is inextricably linked with photosynthesis and microbial activity, anoxia, soil temperature, snowpack, and disturbance regimes (Rodriguez-Iturbe 2000; Hinzman et al. 2005; Chapin et al. 2009; Chapin et al. 2011). My dissertation helps to shed light on widespread boreal lake shrinkage as a recently described ecohydrological feedback, where interactions between hydrological and ecological process, have consequences for biodiversity, wildlife habitat quality, water resources, and C storage. More generally, my research is meant to underline the value of ecohydrology as a conceptual framework for understanding ecosystem responses to climate change (Rodriguez-Iturbe 2000), and to provide useful guidance for management decisions for a warmer and drier future.

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